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Editor
Dr F.W. GESS: 1978

Contribution to the taxonomy of the southern African species of *Ampulex* Jurine (Hymenoptera: Sphecidae: Ampulicinae)

by

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(Albany Museum, Grahamstown)

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ABSTRACT

Descriptions are given of four new species of southern African *Ampulex*, namely *bantuae*, *lesothoensis*, *montivaga* and *nigrisetosa*. *A. cyanura* Kohl is redescribed. The female of *A. mutilloides (sensu* Arnold) is shown to be specifically distinct from that of *A. mutilloides* Kohl and is renamed *A. timulloides*. A key is provided to the females of those southern African species of *Ampulex* in which the pronotum is not posteriorly raised into a conical tubercle.

INTRODUCTION

The writing of the present paper was occasioned in the first place by the need to provide a name for an undescribed species of *Ampulex*, aspects of the ethology of which are the subject of a paper shortly to be published. Initially the species in question was believed to be *A. cyanura* Kohl or a species closely allied to it and consequently was cited in print either as *A. cyanura* Kohl or as *A.* sp. near *cyanura* Kohl. When the author was subsequently enabled to compare his specimens with the type of *A. cyanura* Kohl it was immediately apparent that

though superficially similar they were specifically distinct. Characters of importance in distinguishing between the two species received no or at best scant attention in both Kohl's original description of *A. cyanura* and Arnold's subsequent rediscription. It has been found necessary therefore not only to describe the new species but also to redescribe *A. cyanura*. At the same time it has been considered relevant to describe three further species represented in the Albany Museum collection, all of which are seemingly allied to *A. cyanura* and all of which are apparently new.

A. cyanura and the four new species are all medium-sized (length of females 10–16 mm) and are predominantly blue or green lustred (sometimes purple lustred in death). All are further characterized as belonging to that group of species in which the pronotal collar is not posteriorly raised into a conical tubercle. In order to facilitate the identification of the new species a revision was undertaken of that part of Arnold's 1928 key dealing with those species belonging to the above indicated group. It was therefore pertinent to deal also with a confusion in the literature concerning two species known under the name *A. mutilloides*.

Characters found useful in distinguishing species have largely been concerned with the head—its overall shape and more particularly details of the frontal lobes, frontal carinae, mandibles, clypeus and labrum. These features have all been figured.

TAXONOMIC DESCRIPTIONS AND DISCUSSIONS

Ampulex cyanura Kohl

Ampulex cyanura Kohl, 1893: 471, 493, fig. 48, ♀; Arnold, 1928: 206–207, figs 7,7a–d and f, Pl.VIII, fig. 5, ♀, ♂; Callan, 1976: 232 [*partim*, Callan's material only].
Ampulex capensis Cameron, 1905: 254, ♀(?)
Ampulex africana Cameron, 1905: 256, ♂.
[*non*] *Ampulex cyanura* Kohl, Callan, 1976: 232, Gess' prey record [applies to *Ampulex bantuae* **sp. nov.**].

Female (Figs 1, 8, 13 and 18)

Length 14–16 mm (Holotype 15,5 mm)

Head, thorax, abdominal tergites 1–3 and corresponding sternites, coxae partially (especially outer lateral aspect of fore-coxae and dorsal aspects of meso- and metacoxae, not ventral aspects), fore and hind femora and under surface of middle femora, dorsal aspect of hind tibiae *black with metallic blue or green lustre* (purplish in long dead specimens).

Anterior edge of frontal lobes, antennae, median part of clypeus distally, undersides of all coxae, dorsal and lateral aspects of middle femora, fore and middle tibiae, hind tibiae (other than for dorsal aspect), tarsomeres of all legs (other than for ferruginous parts) shining *black without metallic blue or green lustre*.

Mandibles, labrum, apices of first three tarsomeres, most of fourth tarsomere, apex of fifth tarsomere, hind margins of second and third tergites and sternites laterally, normally hidden parts of rest of abdominal segments *ferruginous*.

Wings almost hyaline or somewhat browned (in which case the forewings are darker than the hindwings), beset with semi-erect brown setae the density of which is proportional to the amount of brown pigment in the darker areas of the the wing. Dark areas include: the distal end of the medial cell at RS and the distal end of the submedial cell and the surrounds of the junction of M and Cu-A; in ill-defined cloud extending over the marginal (= radial) cell, the distal half of the first submarginal (= cubital) cell, the entire second submarginal cell, the proximal half or less of the third submarginal cell, and the middle of the second discoidal cell.

The vestiture consists of short decumbent and semi-decumbent white hairs and of longer upright hairs of two distinct types: stiff coarse black hairs and soft white hairs.

The black pilosity occurs on the anterior margin of the clypeus (where forwardly pointing), the antennal scape, the frontal lobes, the frons, vertex and occiput, the pronotal collar, the scutum, scutellum, disc of the metanotum, the pleura and ventral surface of the mesothorax, the coxa, trochanter, femur, tibia and tarsomeres of all the legs, and sternite 2 (where very sparse).

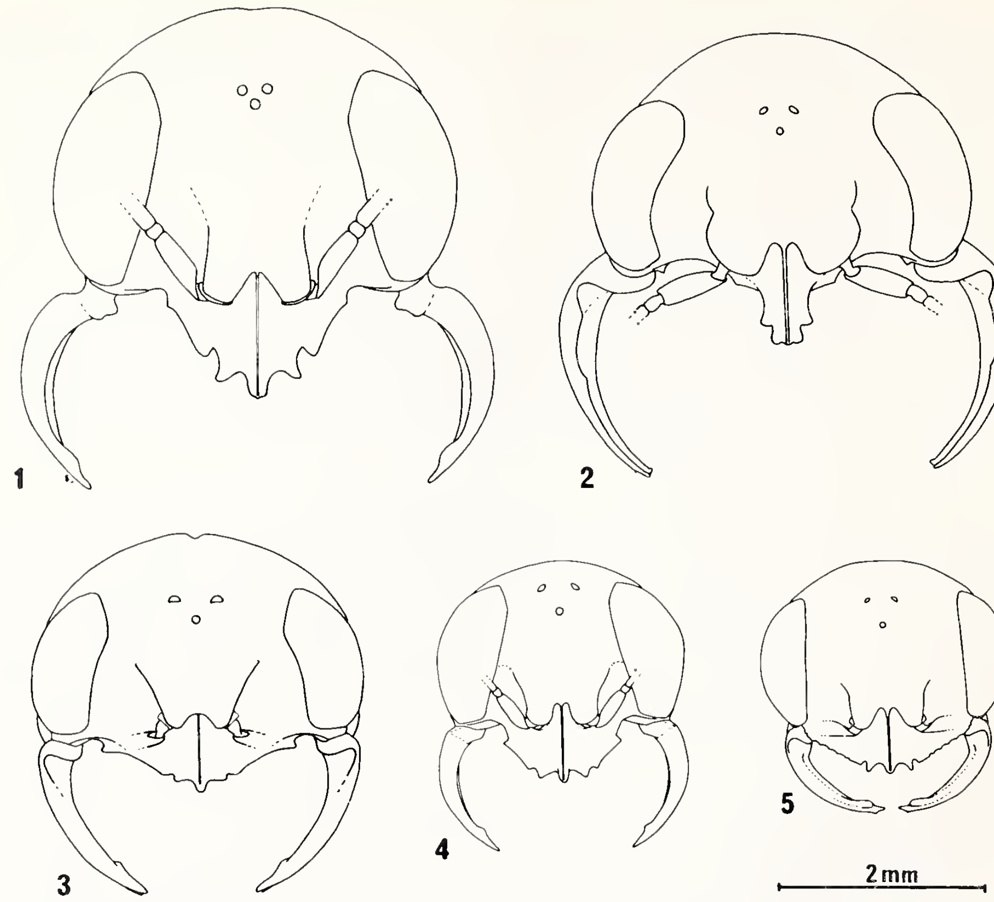
The white upright pilosity occurs on the pleura and ventral surface of the mesothorax (in which areas it is intermixed with black hairs), on the metapleura, and on the sides and declivity of the propodeum.

Short decumbent white hairs densely cover the basalar lobe (where the hairs form a tuft) and the postero-ventral extremities of the meso- and metapleura.

Puncturation of frons strong, coarse and close with diameter of individual punctures about half that of ocelli; puncturation of head behind ocelli and on vertex with individual punctures larger and with shining interstices between them; pronotum, scutum, scutellum and mesopleura with punctures as large as those on vertex, on the pronotum as dense as on the vertex but more sparse on the scutum and scutellum; tergite 1 and 2 shining, sparsely, shallowly and finely punctured; lateral areas of tergite 2 more closely punctured and basal half of tergite 3 very closely and finely punctured.

Head (Fig. 1). Frontal lobes well developed, moderately raised laterally, not expanded laterally and in dorsal view not covering antennal sockets; frontal carinae diverging posteriorly, evanescent far below level of anterior ocellus. Clypeus (Figs 1 and 8) with elevated and produced median part markedly tectiform, strongly carinate in mid-line and strongly and smoothly curved in profile; anterior median tooth strongly developed, its apex smoothly rounded; lateral teeth large, antero-laterally directed, acutely rounded; lateral wings of clypeus well developed, antero-laterally directed and with their free edges smooth, separated from lateral teeth by a deep emargination and terminating abruptly posteriorly and separated from mandibular socket by a deep emargination. Labrum (Figs 8 and 13) robust, with median part greatly produced and by far exceeding strongly downcurved lateral wings which flank it basally; median part in dorsal view outcurved laterally and wider in distal half than in proximal half, its anterior margin widely bilobed and slightly downcurved, its upper surface generally flat and its ventral surface noticeably concave due to lateral thickening; lateral wings each produced into a downwardly directed lamellate lobe inferior in size to lobes of median part; emargination between lateral wing and median part of labrum with three downwardly directed, short, stout and bluntly rounded spatulate setae. Mandibles (Figs 1 and 18) robust, not compressed nor wide in lateral view, distinctly downturned near apex, with a well developed emargination or notch dorsally at the base, with a bluntly triangular lamelliform projection of lower edge just beyond mid-length, with a small tooth immediately below and behind bluntly rounded apex and with a small subapical lamellate cusp on inner surface near upper edge, with a row of short setae below cusp and at base of lamelliform projection and few longer setae on inner surface near base.

Pronotal collar broader than long, *less than twice* (1,5–1,7) as wide behind as long in the mid-line, shorter than scutum; dorsum of collar plain, without a conical elevation but with a moderate and anteriorly deepened and widened longitudinal sulcus in mid-line; scutum with notauli extending to posterior margin; scutellar disc less than twice as wide basally as long in the mid-line; metanotal disc moderately raised, not expanded posteriorly; propodeum *less than twice* (1,8) as wide across base as long in the mid-line of its dorsal face, narrowed posteriorly (0,8 times as wide across postero-lateral teeth as across base); propodeal dorsum with a median longitudinal carina (only evident proximally) and four pairs of posteriorly converging lateral carinae; first (innermost) pair moderately lamelliform, inwardly sloping, shagreened, not attaining hind end of dorsum; second pair not joining nor attaining hind end of dorsum; third pair joining posteriorly across propodeal angle and marking end of dorsum; fourth pair not lamelliformly produced below spiracles.



Figs 1–5. Frontal view of head of: 1, ♀ *A. cyanura* Kohl; 2, ♀ *A. bantuae* sp. nov.; 3, ♀ *A. lesothoensis* sp. nov.; 4, ♀ *A. montivaga* sp. nov.; 5, ♀ *A. nigrisetosa* sp. nov..

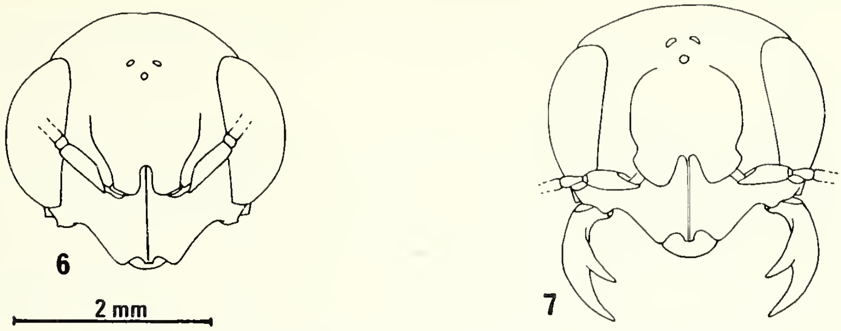
Tergite 1 widest in posterior half, *less than twice* (1,8–1,9) as wide there as long in the mid-line; tergite 2 about as wide in the anterior half (where widest) as long in the mid-line, less than twice (1,8) as long as tergite 1 and only marginally wider.

Forewing with three submarginal (= cubital) cells, with second submarginal cell clearly longer (1,4–1,5) on the media than on the radius.

Male (Fig. 6)

Length 9,8–10,6 mm

Easily associable with the female by the following shared characters: the form of the frontal lobes and frontal carinae; the form of the pronotal collar; the absence on the metanotal disc of any upright white pilosity and of a dense covering of decumbent white hairs; the simple (non-lamelliform) nature of the fourth pair of lateral carinae of the propodeal dorsum; the proportions of the second submarginal cell of the forewings.



Figs 6–7. Frontal view of head of: 6, ♂ *A. cyanura* Kohl; 7, ♂ *A. bantuae* sp. nov..

Material examined: Cape Province: K.b.sp. [= Cap bonae spei], no date (no collector), Holotype ♀ (bearing label: '*cyanura* det. Kohl Type') (Zool. Mus. Berlin); Addo, 19.iv.1896 (Dr Brauns) ♀ (bearing label in Brauns' handwriting: '*Ampulex cyanura* Kohl ♀ confirmed by Kohl himself') (South African Museum ex National Museum Bulawayo 1981); Addo, 19.iv.1896 (Dr Brauns) ♀ (South African Museum ex National Museum Bulawayo 1981); Addo, 19.iv.1896 (Dr Brauns) ♀ (bearing label in Brauns' handwriting: '*A. cyanura* Kohl ♀') (Albany Museum); Grahamstown, Howison's Poort, 7–14.ii.1972 (F. W. Gess, Malaise trap) ♀ (Albany Museum); Grahamstown, Hilton, 5–9.xi.1970, ♂, 12–30.xi.1970, 2♂♂ (all F. W. Gess, Malaise trap) (Albany Museum); Grahamstown, Kudu Reserve (33° 08'S, 26° 42'E), 28.xii.1981 (P. G. Hawkes & P. M. C. Croeser) ♀ (In dry river bed bordered by flowering *Acacia karroo*) (Albany Museum).

Zululand: Mfongosi, viii.1911 (W. E. Jones) ♀ (bearing label in Arnold's handwriting: '*Ampulex cyanura*') (South African Museum); Mfongosi, i.1917 (W. E. Jones) ♀ (bearing label in Arnold's handwriting: '*Ampulex cyanura* Kohl (= *capensis* Cam.) (= *africana* Cam.) ♀ A. Tr. Mus. XII III 1928, 206') (South African Museum).

Ampulex bantuae sp. nov.

Ampulex cyanura (*non* Kohl) Callan, 1976: 232 [*partim*, Gess' prey record only].
Ampulex sp. near *cyanura* Kohl, Gess, 1981: 29, 72–77, fig. 36; Gess & Gess, 1981: 27–30, fig. 2.

Female (Figs 2, 9, 14 and 19)

Length 11,5–14,5 mm (commonly 13,0–13,3 mm; Holotype 14,5 mm)

Head, thorax, abdominal tergites 1–4 and corresponding sternites, coxae, femora and tibiae of all legs, first tarsomere of metathoracic leg, usually first tarsomere of mesothoracic leg and occasionally first tarsomere of prothoracic leg, *black with metallic blue lustre* (sometimes purplish in dead specimens).

Anterior edge of frontal lobes, antennae, nasiform median part of clypeus basally, tarsomeres other than those listed above, basal half of claws, exposed parts of terminal abdominal segments, *shining black without metallic blue lustre.*

Mandibles *bright ferruginous*, sometimes darker at edges, contrasting strongly with metallic blue cheeks. Apical half of nasiform portion of clypeus (usually), clypeal teeth and narrow lateral parts of clypeus, labrum and apical half of tarsal claws *dark ferruginous*. Maxillary and

labial palps *dark brown.* (It should be noted that the extreme hind margins of the abdominal tergites and sternites from the second segment onwards may occasionally show ferruginous colour. In an extended abdomen the normally hidden basal parts of the segments are likewise ferruginous.)

Wings hyaline or slightly browned, beset with semi-erect brown setae the density of which is proportional to the amount of brown pigment in the darker areas of the wing. Dark areas include: a longitudinal streak in the medial cell, most of the submedial cell, the lower proximal corner of the subdiscoidal cell and part of the wing membrane posterior to these two cells; the marginal (= radial) cell, the distal half of the first submarginal (= cubital) cell, the entire second submarginal cell, the proximal half of the third submarginal cell and a diffuse band across the middle of the second discoidal cell.

The vestiture consists of short decumbent and semi-decumbent white hairs and of a mixture of longer upright hairs of two distinct types: relatively longer stiff black hairs and relatively shorter soft white hairs.

The black pilosity occurs on the frons and vertex, the dorsal aspect of the pronotum, the scutum, scutellum, posterior margin of the metanotal disc and parts of the legs (notably the dorsal and outer aspects of the tibiae and first tarsomeres).

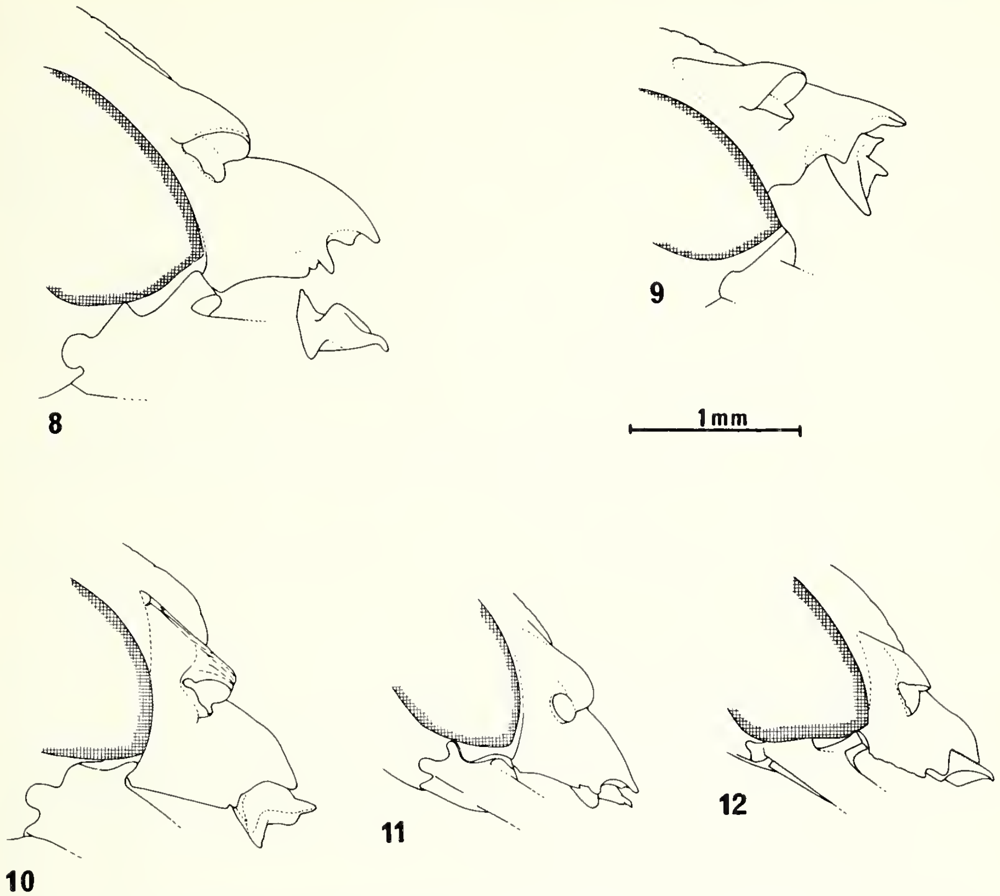
The white pilosity occurs on the occiput, sides and underside of the head, the anterior declivity, sides and ventral surface of the prothorax, the metanotal disc, the pleura of the meso- and metathorax and the ventral surface of these segments, the sides of the propodeum, the lower half of the propodeal declivity (particularly towards the sides), tergites 1-3 (where sparse and mostly on the sides and posterolateral corners) and sternite 2. It is also present on the coxa, trochanter, femur, tibia and first tarsomere of each leg.

Long stiff forwardly-pointing ferruginous hairs are present on the clypeus; shorter ferruginous hairs occur on the labrum and mandibles. Black hairs shorter than those described above are present on the antennal scapes and first five or six flagellar segments; common on the scape and second flagellar segment, the hairs become progressively shorter and sparser with each succeeding segment.

Short decumbent white hairs densely cover the disc of the metanotum, the basalar lobe (where the hairs form a tuft), the posteroventral extremities of the meso- and metapleura, the dorsal aspect of the metacoxae, the posterior margin of tergite 2 laterally and the adjacent lateral part of the hind margin of sternite 2. Similar hairs but a lot less dense occur laterally on the hind margins of tergite 3 and sternite 3 and may occasionally form a small patch situated on the posterior third of the pronotum in the midline.

Puncturation of frons and vertex reticulate, very coarse and close with diameter of individual punctures about $\frac{3}{4}$ that of ocelli and without interstices between punctures; gena with smaller oval punctures and smooth interstices; pronotum, scutum, scutellum and mesopleuron with oval punctures similar in size to those of gena and separated by shining interstices equalling or exceeding the punctures in size; tergite 1 and most of 2 highly polished and shiny with small punctures separated by 2–4 times their diameter and with midline of the segments almost inpunctate; postero-lateral areas of tergite 2 and whole of tergite 3 very closely and finely punctured and with a scattering of larger punctures; dorsal aspect of tergites 4 and 5 with minute punctures, tergite 6 virtually impunctate.

Head (Fig. 2). Frontal lobes well developed, only weakly raised laterally, arcuately expanded laterally and in dorsal view completely covering antennal sockets; frontal carinae parenthesis-like, evanescent well below level of anterior ocellus. Clypeus (Figs 2 and 9) with elevated and produced median part markedly nasiform, carinate in mid-line and only weakly curved in profile; median part sub-parallel-sided distally, apically not tooth-like but wide and somewhat flattened, subtruncate and very weakly trilobed; lateral teeth large, downwardly directed, acutely rounded; lateral wings of clypeus poorly developed, downwardly rather than



Figs 8–12. Lateral view of anterior part of head of: 8, ♀ *A. cyanura* Kohl; 9, ♀ *A. bantuae* sp. nov.; 10, ♀ *A. lesothoensis* sp. nov.; 11, ♀ *A. montivaga* sp. nov.; 12, ♀ *A. nigrisetosa* sp. nov..

antero-laterally directed and thus appearing to be strongly receding when seen from above, with a slight angle in region below antennal socket and with free edge thinly lamelliform. Labrum (Figs 9 and 14) robust, triangular in overall shape, greatly but regularly widened from base to apex and with extensive lateral wings exceeding median part, almost three times as wide across acute antero-lateral angles (i.e. apices of lateral wings) as long in the middle; median part raised above level of lateral wings over its entire length and strongly conically produced in basal half where furnished with a high pointed tubercle, its apical margin weakly bilobed with a small backwardly pointing median tooth; emargination between lateral wing and median part of labrum with a pair of forwardly directed, short, stout and bluntly rounded spatulate setae.

Mandibles (Figs 2 and 19) robust, compressed, wide in lateral view, widest a little beyond midlength but lacking any lamelliform projection of lower edge and neither downturned near apex nor having a subapical tooth, with a well developed emargination dorsally at the base but

with the part basad to emargination not produced over the latter to form an acute notch, with the interior upper edge in dorsal view not a smooth curve but in three steps, with two small inwardly directed cusps on apex (at least in newly emerged individuals).

Pronotal collar broader than long, *more than twice* (2,1–2,3) as wide behind as long in the midline, shorter than scutum: dorsum of collar plain, without a conical elevation but with a narrow, shallow and even longitudinal sulcus in the midline; scutum with notauli extending to posterior margin; scutellar disc slightly more than twice as wide as long in the midline; metanotal disc moderately raised, expanded posteriorly and therefore exceeding lateral wings in breadth; propodium *more than twice* (2,3) as wide across base as long in the midline of its dorsal face, narrowed posteriorly (0,7 times as wide across postero-lateral teeth as across base); propodeal dorsum with a median longitudinal carina (only evident proximally) and with four pairs of posteriorly converging lateral carinae; first (innermost) pair markedly lamelliform, inwardly sloping, shagreened and contrasting with very shiny areas on either side, not attaining hind end of dorsum; second pair joining posteriorly across propodeal angle and marking end of dorsum; fourth pair lamelliformly outwardly and upwardly produced at their origins below spiracles.

Tergite 1 widest in posterior half, *more than twice* (2,1–2,4) as wide there as long in the midline; tergite 2 evenly curved laterally in dorsal view, about one and a quarter times as wide in the middle (where widest) as long in the midline, twice as long as tergite 1 and about one and one-tenth as wide.

Forewing with three submarginal (= cubital) cells, with second submarginal cell subquadrate and only one and one-fifth as long on media as on radius.

MALE (Fig. 7)

Length 7,8–12,0 mm (commonly 10–11 mm; Allotype 11,3 mm)

Easily associable with the female by the following shared characters: the form of the frontal lobes and frontal carinae; the form of the pronotal collar; the possession of a mixture of longer upright hairs of two distinct types; the presence of a dense covering of short decumbent white hairs on the metanotum; the form of the first pair of lateral carinae of the propodeal dorsum; the lamelliform nature of the fourth pair of lateral carinae of the propodeal dorsum; the subquadrate second submarginal cell of the forewings.

MATERIAL EXAMINED: Cape Province: Grahamstown, 29.iv.1966 (C. Jacot-Guillarmod) ♀,♂; Grahamstown, Hilton, 19–23.xi.1975, ♀, 16.xi.1977, ♂ (both F. W. Gess, Malaise trap), 27.xii.1973, ♀, 26.ii.1974, ♀, 15.iii.1974, ♀, 19.xi.1976, ♀, 9.xii.1976, ♀ (all F. W. & S. K. Gess) (all captured in the field, in association either with natural nests or with trap-nests), 10.xi.1977 (F. W. Gess) ♂ (on flowers of *Lasiospermum bipinnatum*, Compositae). In addition to the above specimens, all of which were collected as adults, there are in the Albany Museum collection a further 32♀♀ and 49♂♂ which were reared from eggs, larvae or pupae obtained from natural nests at Hilton, from trap-nests at Hilton, and from laboratory-based trap-nests which had been utilized by caged wasps of the Hilton population. Both the Holotype ♀ and the Allotype ♂ belong to the reared material.

Holotype ♀: Reared from the cockroach *Bantua dispar* (Burmeister) collected (dead) during April, 1975, at Hilton from an old gallery of *Ceroplesis hottentota* (F.) (Cerambycidae) in *Acacia karroo*. Wasp emerged 18.xii.1975.

Allotype ♂: Reared from the cockroach *Bantua dispar* (Burmeister) collected (live) on 25.xi.1973 at Hilton from a trap-nest in *Acacia karroo*. Wasp emerged 21.i.1974.

Paratypes: 38♀♀, 51♂♂ (the bulk of the above listed material).

Etymology: The name is derived from a southern African cockroach genus, *Bantua* Shelford (Blattariae: Derocalyminidae), a species of which, *B. dispar* (Burmeister), is the only known prey of the wasp.

In the South African Museum collection were found two specimens determined as *A. cyanura* which upon examination proved to be *A. bantuae.* Label data and comments are given below:

(a) Cape Province: Mossel Bay, i.1899 (T. W. Overbeek) ♂ (bearing label in Brauns' handwriting: '*Ampulex cyanura* Kohl ♂'). The specimen is without any doubt an *A. bantua* ♂.

(b) Cape Province: Vryburg, 190? (E. Jons) ♀ (bearing label in Arnold's handwriting; '*Ampulex cyanura* Kohl r. *rhodesianus* Arn. ♀'). The specimen is definitely not what it is labelled. Though in the ferruginous colouration of its clypeus, of the anterior parts of its frontal lobes and of its first antennal segment it is similar to the subspecies *rhodesianus*, it differs from it and from *A. cyanura sensu stricto* in the shape of the clypeus and labrum, in the form of the frontal lobes and the mandibles, in the proportions of the pronotum *etc.* In all these characters it agrees closely with *A. bantuae* of which it would appear to be a slight geographical variety.

Ampulex lesothoensis sp. nov.

Female (Figs 3, 10, 15 and 20)

Length 13 mm

Head, thorax, abdomen, all legs to end of femur, hind tibiae dorsally *black with metallic blue, green or purple lustre.* (As with other species also, it appears that not only does the metallic lustre turn from blue or green to purple but the underlying basic black fades to a rich mahogany or ferruginous. It is possible that in a live specimen all the tibiae may be lustred.)

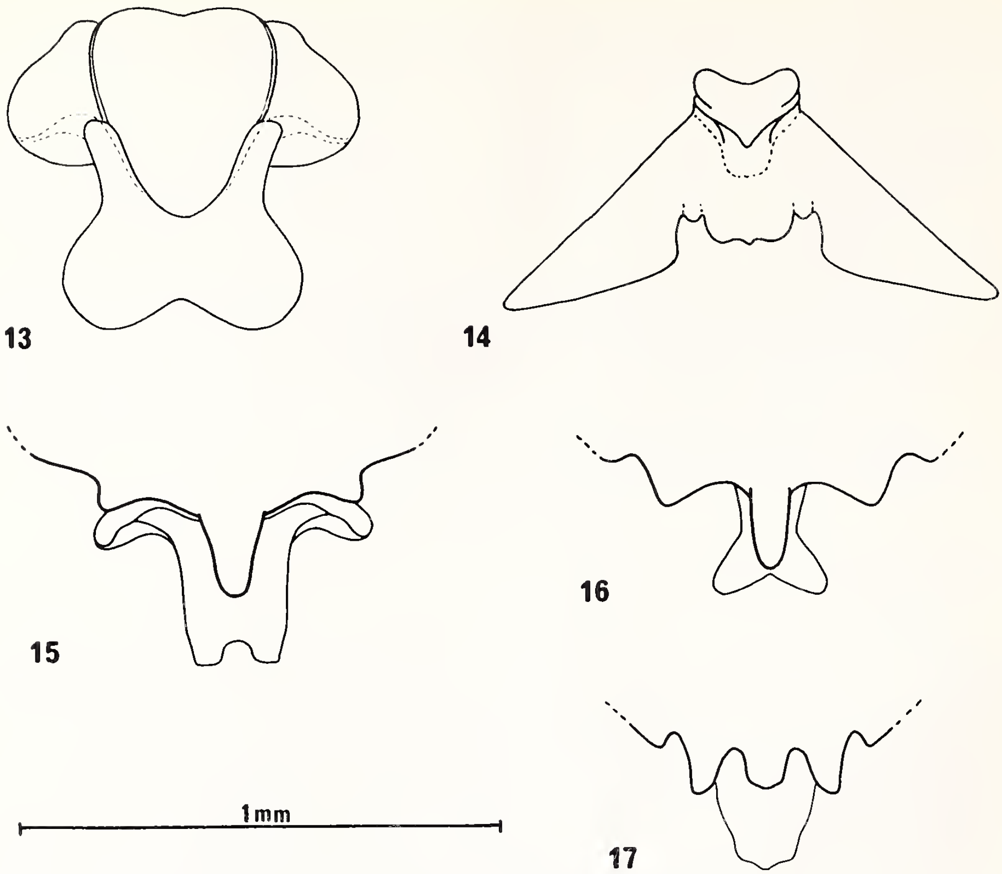
Antennae (including scapes), median projection of clypeus, labrum, palps, mandibles, tibiae and tarsi and normally hidden parts of abdominal segments dark *ferruginous.*

Wings strongly and fairly uniformly browned, without noticeable fasciae, beset with short semi-erect brown setae.

The vestiture consists in the main of sparse very short decumbent white hairs and of longer upright stiff but fine black hairs, the latter occurring on the head, thorax, propodeum, abdomen (where extremely sparse), antennal scapes and first two flagellar segments. Somewhat longer coarser forwardly directed ferruginous hairs are present on the clypeus; shorter ferruginous hairs are present sparsely upon the mandibles. Short decumbent white hairs densely cover the posteroventral extremities of the meso- and metapleura.

Puncturation of frons and vertex reticulate; reticulum on frons fine and without interstices between punctures, becoming less fine at level of ocelli and course with moderately shining interstices between elongate punctures on vertex; punctures on gena large and elongate with shining interstices; pronotum, scutum, scutellum and mesopleuron with large coarse punctures similar in size to those of gena; tergites and sternites highly polished and shiny all over and fairly uniformly covered with small shallow and widely separated punctures.

Head (Fig. 3). Frontal lobes well developed, very strongly raised laterally, not expanded laterally and in dorsal view not covering antennal sockets; frontal carinae strongly divergent posteriorly, strongly raised over their entire length and ending abruptly far below level of anterior ocellus. Area between frontal carinae somewhat elevated medially. Clypeus (Figs 3 and 10) with elevated and produced median part tectiform, weakly carinate in mid-line and moderately curved in profile; anterior median tooth moderately developed, its apex acutely rounded; lateral teeth moderately developed, antero-laterally directed, rounded, well separated



Figs 13–17. Frontal view of entire labrum (Figs 13–14) or of anterior part of labrum (Figs 15–17) of: 13, ♀ *A. cyanura* Kohl; 14, ♀ *A. bantuae* sp. nov.; 15, ♀ *A. lesothoensis* sp. nov.; 16, ♀ *A. montivaga* sp. nov.; 17, ♀ *A. nigrisetosa* sp. nov..

from median tooth; lateral wings of clypeus well developed, antero-laterally directed and with their free edges smooth and slightly upturned, weakly separated from lateral teeth by narrow and shallow emargination and terminating abruptly posteriorly and separated from mandibular socket by a deep emargination. Labrum (Figs 10 and 15) robust, with median part greatly forwardly produced and by far exceeding strongly downcurved lateral wings which flank it basally; median part more or less square in crosssection, in dorsal view with sides subparallel (converging very slightly anteriorly) and with upper apical margin pointedly bilobed, with apical face concave and ventral face flat; downcurved lateral wings lamelliform distally, widely rounded and superior in size to apical lobes of median part; emargination between lateral wing and median part of labrum with a pair of downwardly directed, short, stout and bluntly rounded spatulate setae. Mandibles (Figs 3 and 20) robust, not compressed, narrowed towards apex and slightly downturned, with a poorly developed emargination dorsally at the base and with part basad to emargination not produced over the latter and not forming an acute notch, with a

very low longitudinal lamelliform ridge projecting from near mid-length to shortly before apex, without a small tooth immediately below and behind apex but with two low cusps on outer surface apically and with apex itself incurved to form a sharp cusp on inner surface, with a large pointed subapical cusp on inner surface near upper edge.

Pronotal collar broader than long, *more than twice* (2,2) as wide behind as long in the mid-line, shorter than scutum; dorsum of collar plain, without a conical elevation but with a wide and deep longitudinal sulcus in the mid-line; scutum with notauli deep and wide and extending to posterior margin; scutellar disc less than twice as wide basally as long in the mid-line; metanotal disc very strongly raised throughout and especially laterally where subtuberculate, not expanded posteriorly; propodeum less than twice (1,9) as wide across base as long in the mid-line of its dorsal face, narrowed posteriorly (0,8 times as wide across postero-lateral teeth as across base); propodeal dorsum with a median longitudinal carina and four pairs of posteriorly converging lateral carinae; first pair moderately developed, sublamelliform, inwardly sloping, not shagreened, not attaining hind end of dorsum; second, third and fourth pairs somewhat indistinct due to coarse reticulate surface sculpturing; second pair not joining nor attaining hind end of dorsum but third pair doing so and continuing around and margining hind edge; fourth pair not lamelliformly produced below spiracles.

Tergite 1 widest in posterior half, *less than twice* (1,8) as wide there as long in the mid-line; tergite 2 about one and one-tenth as wide in the anterior half (where widest) as long in the mid-line, less than twice (1,6) as long as tergite 1 and of the same width.

Forewing with three submarginal (= cubital) cells, with the second submarginal cell clearly longer (1,6) on the media than on the radius.

MALE Unknown.

MATERIAL EXAMINED: Lesotho (formerly Basutoland): Mahlatsa, 30.xii.1951 (A. Jacot-Guillarmod), Holotype ♀ (Albany Museum).
Mahlatsa (29° 11′S, 27° 58′E) is situated in the Berea district of Lesotho in the foothills at an altitude somewhat in excess of 1 800 m. The vegetation is sparse and consists mostly of grass.

ETYMOLOGY: The name, an adjective, is derived from the geographical name, Lesotho, and refers to the provenance of the described specimen.

Ampulex montivaga sp.nov.

FEMALE (Figs 4, 11, 16 and 21)

Length 10–13 mm (Holotype 10 mm)

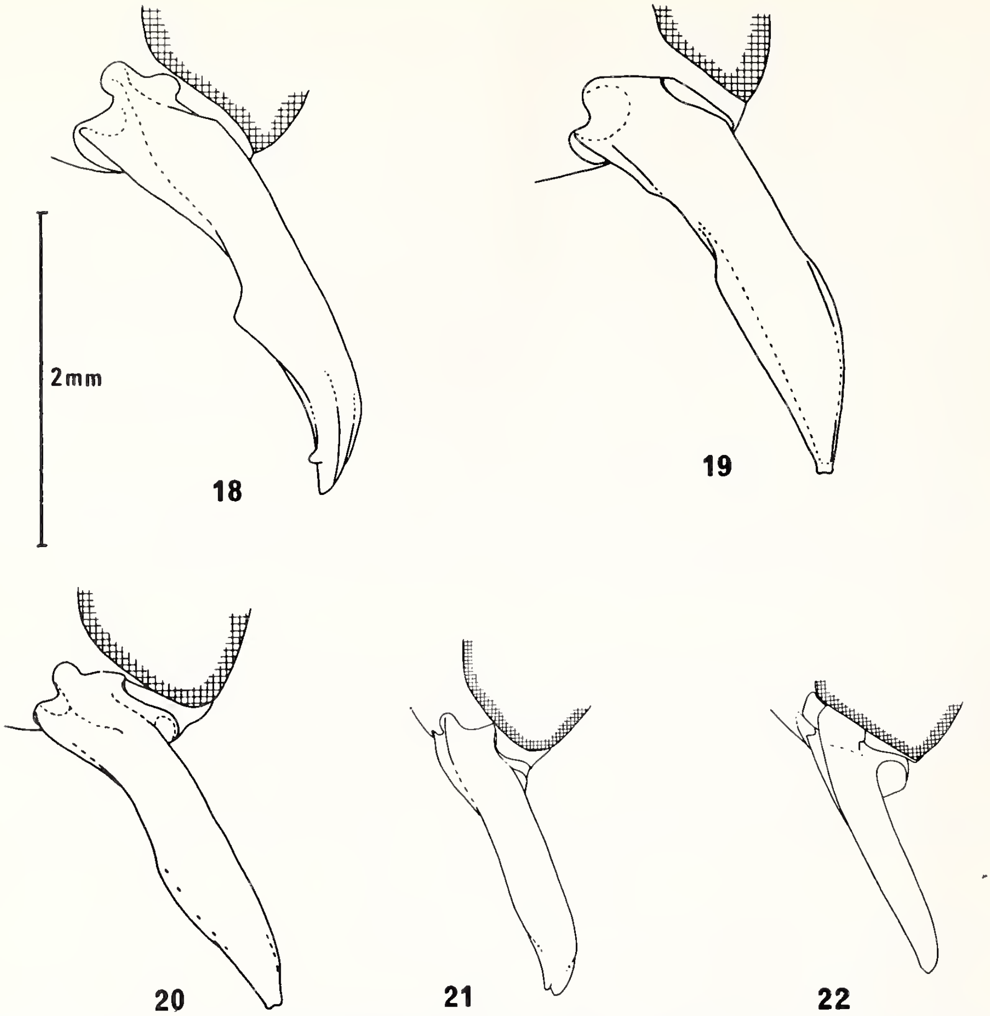
Head, upper surface of scapes, thorax, abdomen, all legs to end of tibia, first tarsomere of metathoracic leg, *black with metallic blue, green or purple lustre.*

Antennae (except for upper surface of scapes), mandibles to a variable extent, tarsomeres (other than blue first tarsomere of metathoracic leg and ferruginous apices of all tarsomeres) *black.*

Mandibles at base and apex, parts of tarsomeres and normally hidden parts of abdominal segments *dark ferruginous.*

Wings subhyaline, very lightly browned, without noticeable fasciae, beset with short semi-erect brown setae.

The vestiture consists in the main of sparse very short decumbent white hairs and of longer upright stiff but fine black hairs, the latter occurring on the head, thorax, propodeum, abdomen (where extremely sparse), legs, antennal scapes and first two flagellar segments. Somewhat longer coarser forwardly directed black hairs are present on the clypeus; shorter



Figs 18–22. Lateral view of right mandible of: 18, ♀ *A. cyanura* Kohl; 19, ♀ *A. bantuae* sp. nov.; 20, ♀ *A. lesothoensis* sp. nov.; 21, ♀ *A. montivaga* sp. nov.; 22, ♀ *A. nigrisetosa* sp. nov..

coarse black hairs are common upon the mandibles. Short decumbent white hairs densely cover the basalar lobe and the postero-ventral extremities of the meso- and metapleura.

Puncturation of frons and vertex reticulate; reticulum on frons close with very narrow shining interstices between punctures, becoming less close at level of ocelli and on vertex coarse with wider shining interstices; pronotum, scutum, scutellum and mesopleura with large coarse punctures similar in size to those of vertex; tergites and sternites of first two abdominal segments highly polished and uniformly covered with small shallow widely separated punctures; tergite 3 more closely punctured expecially basally.

Head (Fig. 4). Frontal lobes well developed, strongly raised laterally, not expanded laterally and in dorsal view not covering antennal sockets; frontal carinae diverging posteriorly, evanescent far below level of anterior ocellus. Clypeus (Figs 4 and 11) with elevated and produced median part markedly tectiform, strongly carinate in the mid-line and weakly but smoothly curved in profile; anterior median tooth well developed, its apex rounded; lateral teeth moderately developed, antero-laterally directed, acutely rounded, well separated from median tooth; lateral wings of clypeus well developed, antero-laterally directed and with their free edges smooth, well separated from lateral teeth by a wide but shallow emargination and terminating abruptly posteriorly and separated from mandibular socket by a narrow but deep emargination. Labrum (Figs 11 and 16) robust, with median part greatly produced and by far exceeding strongly downcurved lateral wings which flank it basally; median part in dorsal view with sides diverging anteriorly and with anterior margin widely bilobed (lobes antero-laterally pointing and noticeably bent down anteriorly), its upper surface more or less flat and its ventral surface concave due to lateral thickening; lateral wings lobate but not lamellately downwardly produced; emargination between lateral wing and median part of labrum with a pair of downwardly directed short, stout and bluntly spatulate setae. Mandibles (Figs 4 and 21) robust, neither compressed nor wide in lateral view and lacking a lamelliform projection of the lower edge, narrowed at apex and distinctly downturned, with a poorly developed emargination or notch dorsally at the base, with a small tooth immediately below and behind apex and with a large pointed subapical lamellate cusp on inner surface near upper edge.

Pronotal collar broader than long, *twice as wide* behind as long in the mid-line, shorter than scutum; dorsum of collar plain, without a conical elevation but with a narrow and shallow longitudinal sulcus in mid-line; scutum with notauli extending to posterior margin; scutellar disc less than twice as wide basally as long in the mid-line; metanotal disc moderately raised, not expanded posteriorly; propodeum less than twice (1,6) as wide across base as long in the mid-line of its dorsal face, narrowed posteriorly (0,8 times as wide across postero-lateral teeth as across base); propodeal dorsum with a median longitudinal carina and four pairs of posteriorly converging lateral carinae; first pair moderately developed, sublamelliform, shagreened, not attaining hind end of dorsum; second, third and fourth pairs indistinct (particularly posteriorly) due to weak development and coarse surface sculturing; second pair not joining nor attaining hind end of dorsum but third pair doing so and continuing around and margining hind edge; fourth pair not lamelliformly produced below spiracles.

Tergite 1 widest in posterior half, less than twice (1,75) as wide there as long in the mid-line; tergite 2 about one and one-tenth as wide in the anterior half (where widest) as long in the mid-line, less than twice (1,75) as long as tergite 1 and about one and one-tenth as wide.

Forewing with three submarginal (= cubital) cells, with the second submarginal cell clearly longer (1,5–1,8) on the media than on the radius.

MALE Unknown.

MATERIAL EXAMINED: Lesotho (formerly Basutoland): Haha-la-Sekhonyana, 30.xii.1946 (N. C. Mokhehle), Holotype ♀, same locality and date (A. Jacot-Guillarmod), Paratype ♀ (both Albany Museum).
Haha-la-Sekhonyana (29° 22′S, 28° 19′E) is situated in the Maseru district of Lesotho in the mountains at an altitude of 2 450–2 750 m. The vegetation, on basalt, is sparse and consists mostly of grass.

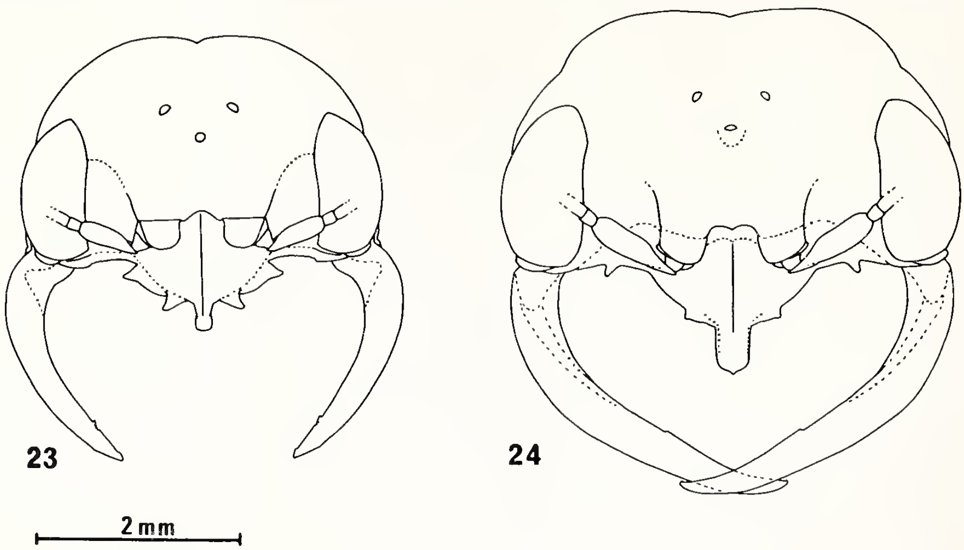
ETYMOLOGY: The name, derived from the word *montivagus -a -um*: wandering over the mountains, refers to the species' occurrence in a mountainous situation.

Ampulex nigrisetosa sp. nov.

FEMALE (Figs 5, 12, 17 and 22)

Length 10–13 mm (Holotype 10,7 mm)

Head, thorax, abdominal tergites 1—3 and corresponding sternites, coxae and femora of all legs and dorsal aspect of tibiae of hind legs *black with metallic blue lustre* (sometimes purplish in dead specimens). (The metallic lustre is poorly developed on the abdomen and legs and is not apparent in all the specimens; sometimes the entire abdomen is lustreless black.) Tibiae of all legs (except for dorsal aspect of hind tibiae) *black*, apparently without metallic lustre; tarsomeres varying from black to dark ferruginous as is the case also with the antennal flagellum.



Figs 23–24. Frontal view of head of: 23, ♀ *A. mutilloides* Kohl; 24, ♀ *A. timulloides* sp. nov..

Mandibles, antennal scapes (at least on underside) and normally hidden parts of abdominal segments *ferruginous*.

Wings lightly browned, beset with semi-erect brown setae the density of which is proportional to the amount of brown pigment in darker areas of the wing. The dark areas include: a longitudinal streak in the medial cell, most of the submedial cell, the proximal edge of the subdiscoidal cell and part of the wing membrane posterior to these two cells; the marginal (= radial) cell, the distal half of the first submarginal (= cubital) cell, the entire second submarginal cell, the proximal half of the third submarginal cell and a diffuse band across the middle of the second discoidal cell.

The vestiture consists in the main of very short sparse decumbent white hairs and of black upright hairs. Long, very coarse and stiff black pilosity occurs on the frons and vertex, on the dorsal surfaces of the pronotal collar, the scutum, scutellum and metanotal disc, and on the hind femora and tibiae; shorter and finer black pilosity occurs on the mesopleura, underside of the pro- and mesothorax, pro- and mesothoracic legs and sternite 2 (where very sparse). Short decumbent white hairs densely cover the basalar lobe and the postero-ventral extremities of the meso- and metapleura.

Puncturation of frons, vertex, genae, pronotum, scutum, scutellum and mesopleura coarse with shining interstices; interstices on dorsum and sides of pronotum strongly raised and fused to form pronounced longitudinal rugae; abdominal tergites moderately covered with small shallow punctures.

Head (Fig. 5). Frontal lobes well developed, moderately raised laterally, not expanded laterally and in dorsal view not covering antennal sockets; frontal carinae low, diverging posteriorly, evanescent far below level of anterior ocellus. Clypeus (Figs 5 and 12) with elevated and produced median part markedly tectiform, strongly carinate in mid-line and strongly curved in profile; anterior median and lateral teeth of equal size, strong and acutely rounded, separated by a deep but narrow emargination; lateral wings of clypeus well developed, antero-laterally directed and with their free edges serrate, separated from lateral teeth by a small emargination and extending posteriorly without interruption and without emargination the entire distance to the mandibular socket. Labrum (Figs 12 and 17) robust, with median part greatly produced and by far exceeding downcurved lateral wings which flank it basally; median part in dorsal view with sides converging anteriorly, with distal end widely rounded (not bilobed) and slightly bent down, with its upper surface more or less flat but its ventral surface progressively raised in the mid-line from apex to base; lateral wings small, not separated from median part as situated underneath base of latter rather than to each side, without lamellate projections but each with three downwardly and slightly inwardly directed, short, stout and bluntly rounded spatulate setae. Mandibles (Figs 5 and 22) robust, not compressed nor wide in lateral view and lacking any lamelliform projection of lower edge, very slightly downturned near apex, with a well developed emargination dorsally at the base but with part basad to emargination though raised hardly produced over the latter and not forming a deep acute notch, with at most a small, low and rounded cusp immediately below and behind apex, with an elongate subapical lamelliform cusp on inner surface near upper edge.

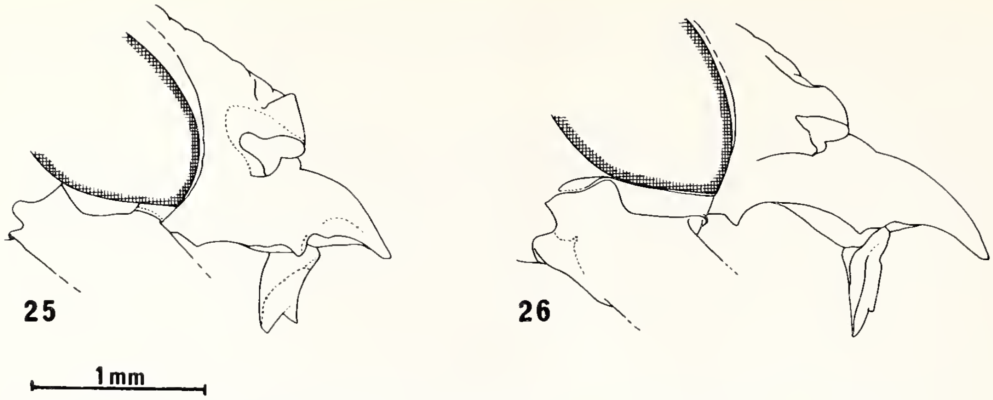
Pronotal collar broader than long, *less than twice* (1,3–1,4) as wide behind as long in the mid-line, *of same length* as scutum; dorsum of collar plain without a conical elevation but with a narrow and mostly shallow longitudinal sulcus in the mid-line; scutum with notauli extending to posterior margin; scutellar disc less than twice (1,75) as wide basally as long in the mid-line; metanotal disc moderately raised, not expanded posteriorly; propodeum less than twice (1,6) as wide across base as long in the mid-line of its dorsal face, narrowed posteriorly (0,8 times as wide across postero-lateral teeth as across base); propodeal dorsum with a median longitudinal carina and four pairs of posteriorly converging lateral carinae; first pair well developed but not lamelliform nor shagreened, not attaining hind end of dorsum; second, third and fourth pairs somewhat indistinct due to coarse reticulate surface puncturing; second pair not joining nor attaining hind end of dorsum but third pair doing so and continuing around and margining hind edge; fourth pair not lamelliformly produced below spiracles.

Tergite 1 widest in posterior half, *less than twice* (1,7) as wide there as long in the mid-line, tergite 2 as wide in anterior half (where widest) as long in the mid-line, almost twice (1,9) as long as tergite 1 and about one and one-tenth as wide.

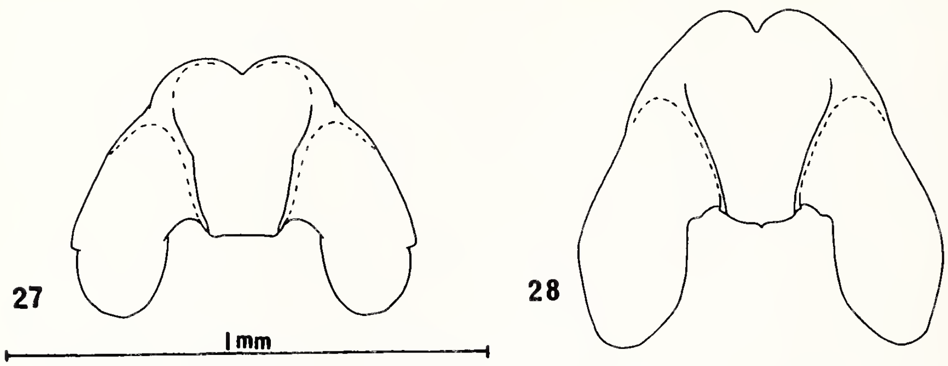
Forewing with three submarginal (= cubital) cells but loss of the first intersubmarginal veinlet (= first transverse cubital vein) in some wings results in only two submarginal cells being present. (In the four specimens examined, one has the veinlet present but weak in both wings, two have the veinlet absent in both wings, and one specimen, the Holotype, has it present in the left-hand wing and absent in the right-hand wing.) Second submarginal cell when present clearly longer (1,5) on the media than on the radius.

Male Unknown.

Material examined: Cape Province: Grahamstown, Avenue Park, 23.iv.1967 (D. Brothers), Holotype ♀ (with prey) (Albany Museum); Grahamstown, Hilton, 21–31.x.1970, 1–16.i.1971



Figs 25–26. Lateral view of anterior part of head of: 25, ♀ *A. mutilloides* Kohl; 26, ♀ *A. timulloides* sp. nov..



Figs 27–28. Frontal view of entire labrum of: 27, ♀ *A. mutilloides* Kohl; 28, ♀ *A. timulloides* sp. nov..

and 17–31.i.1971 (all F. W. Gess, Malaise trap) 3 Paratype ♀♀ (all Albany Museum). The prey taken with the Holotype is a 9,2 mm long apterous female nymph, possibly a species of *Perisphaeria*.

ETYMOLOGY: The name, a combination of two words, is derived from *niger -ra -rum:* black and *setosus -a -um*: bristled, and draws attention to the characteristic setae.

Ampulex mutilloides Kohl

Ampulex mutilloides Kohl, 1893: 456, 468–469, fig. 61, ♀; Arnold, 1928: 205–206, fig. 6 [*partim*, ♂ only]; Jacot-Guillarmod, 1951: 236 (plant visiting); Gess, 1981: 17, 53–54 (speculation re. nesting and prey).
Ampulex sanguinicollis Brauns, 1899: 394–395, ♂.
[*non*] *Ampulex mutilloides* Kohl, Arnold, 1928: 205, fig. 6a, ♀ [= *A. timulloides* **sp. nov.**].

Ampulex mutilloides was described by Kohl (1893: 468–469 and fig. 61) from a single female collected by Drége in South Africa (Afr. austr.). *A. sanguinicollis*, described by Brauns

(1899: 394–395) from a single male collected by himself at Uitenhage not far from Port Elizabeth, was sunk into synonomy with *mutilloides* by Arnold (1928: 205). Arnold's belief that *A. sanguinicollis* represents the male of *A. mutilloides* is supported by the study of material of both males and females collected by Jacot-Guillarmod at Mamathes in Lesotho where the species appears to be not uncommon. In his revision of the Sphecidae of South Africa Arnold (1928: 205–206, figs 6, 6a) in dealing with *A. mutilloides* gave new descriptions in English of both sexes, the original descriptions of both Kohl and Brauns having been in German. It is clear from Arnold's statement (1922: 104) that the material which he had at his disposal included Brauns' but not Kohl's types. Arnold's description of the female was therefore based not upon Kohl's type but upon new material believed by him to be *A. mutilloides* and consisting of two females from the Transvaal, one from Carolina and the other from Pretoria.

Comparison of Kohl's and Arnold's descriptions and figures pertaining to the female show considerable descrepancies of which the most immediately obvious involve the puncturation of the head and the form of the clypeus. Concerning the puncturation Kohl stated: "Kopf gross und wie der Thorax dicht und ungemein grob . . . punktirt; zwischen den Punkten verlaufen Runzeln" (head large and like the thorax closely and unusually coarsely punctured; between the punctures run wrinkles). Arnold, on the other hand, stated: "Head strongly and rather irregularly punctured; the punctures smallest on the middle of the face and on the temples, on the face fairly far apart; the sides of the face are closely punctured and somewhat rugose. The vertex and occiput have widely spaced, large and deep punctures, the spaces between them smooth and shining". With respect to the clypeus, that figured by Kohl (fig. 61) appears to be very different from that figured by Arnold (fig. 6a). The suspicion is therefore aroused that the females from Carolina and Pretoria purported to be *A. mutilloides* are not in fact conspecific with Kohl's female but rather represent a closely related but distinct species.

Examination of the specimens included under *A. 'mutilloides'* in the Albany Museum and in the South African Museum collections (the latter holding Arnold's material formerly belonging to the National Museum in Bulawayo) showed that, of the total of eighteen females, fourteen could be assigned to *A. mutilloides sensu* Kohl and four to *A. mutilloides sensu* Arnold and that the differences between the two groups of specimens were sufficient to warrent specific separation.

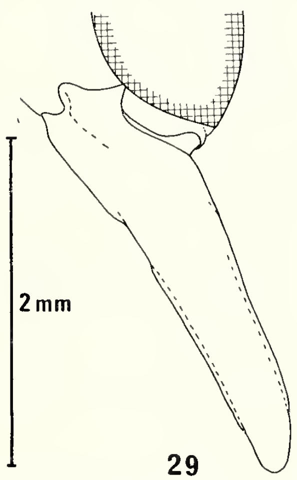


Fig. 29. Lateral view of right mandible of ♀ *A. mutilloides* Kohl.

The four females answering to *A. mutilloides sensu* Arnold are assigned to *A. timulloides* sp. nov.. Major differences between *A. mutilloides* and *A. timulloides* are discussed below under the latter species.

Figure citations, measurements and list of examined material given immediately below pertain to *A. mutilloides* Kohl.

FEMALE (Figs 23, 25, 27 and 29)

Length 10,5–16,5 mm (average of 15 specimens 13,4 mm)
Adequately described by Kohl (*loc. cit.*).

MALE

Length 7,1–11,1 mm (average of 15 specimens 9,1 mm)
Adequately described by Brauns and by Arnold (*loc. cit.*).

MATERIAL EXAMINED: Cape Province: Algoa Bay, no date (Dr Brauns) ♀ (South African Museum ex National Museum Bulawayo 1981); Aliwal North, x.1945 (N. C. Mokhehle) ♀ (Albany Museum); Grahamstown, 20.iii.1969 (J. Pringle) ♀ (Albany Museum); Grahamstown, Hilton, 25.i.1974 (F. W. & S. K. Gess) ♀ (Albany Museum). Lesotho (formerly Basutoland): Mamathes, Sept.–Jan., 1942–1953 (C., A. & F. Jacot-Guillarmod, D. Wickham and N. C. Mokhehle) 8♀♀, 14♂♂ (5♀♀, 12♂♂ in Albany Museum; 3♀♀, 2♂♂ in South African Museum ex National Museum Bulawayo 1981). Natal: Frere, iii.1891 (G. A. K. Marshall) ♂ (South African Museum). Zimbabwe (formerly S. Rhodesia): Salisbury, iv.1913 (no collector) ♀ (South African Museum). No locality, no date (no collector) 2♀♀ (Albany Museum).

Ampulex timulloides sp. nov.

Ampulex mutilloides (*non* Kohl) Arnold, 1928: 205, fig. 6a [*partim*, ♀ only].

FEMALE (Figs 24, 26 and 28)

Length 14,8–18 mm (average of 4 specimens 16,2 mm; Holotype 18 mm)

Adequately described by Arnold (*loc. cit.*) (as *mutilloides*), it is very similar in colouration and general facies to *A. mutilloides* Kohl from which it may, however, be readily distinguished on the basis of the characters which follow.

The head (Fig. 24) is of relatively greater width than that of *A. mutilloides* (Fig. 23), its width across the eyes being equal to *c.* 0,29 of the total body length as opposed to *c.* 0,26. However, as accurate measurement of the total body length is complicated by factors such as varying degrees of body flexion and of abdominal telescoping, head width is better compared to a body measurement not subject to such variations. Thus in Fig. 30 the width of the head across the eyes is plotted against the length from the anterior margin of the scutum to the brink of the propodeal declivity measured along the dorsal midline. Regression lines fitted to the sets of points show that whereas the relationship of head width to scutum-propodeal declivity length is consistent within each species, the relative head width of *A. timulloides* is consistently greater.

The vertex and occiput have widely spaced, large and deep punctures, the spaces between them being smooth and shining whereas in *A. mutilloides* the vertex and occiput have close and coarse punctures separated by rugae.

The lateral wings of the clypeus are poorly developed and receding (Figs 24 and 26). Anteriorly they are in the same plane as the lateral teeth from which they are not separated but from which they extend in a smooth, very shallow and extremely wide curve to their weakly or

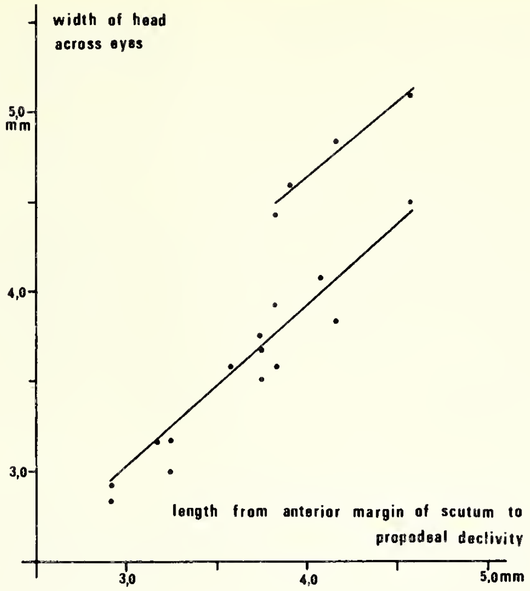


Fig. 30. Regression lines fitted to width, in mm, of head across eyes (vertical axis) plotted against length, in mm, from anterior margin of scutum to brink of propodeal declivity measured along dorsal midline (horizontal axis) for 4 females of *A. timulloides* sp. nov. (above) and 14 females of *A. mutilloides* Kohl (below).

only moderately produced tooth-like postero-lateral extremities. In *mutilloides*, by contrast, the lateral wings (Figs 23 and 25) are well developed and produced. Anteriorly they are in a plane distinct from that of the lateral teeth from which they are also clearly separated. Arising from behind and slightly below the level of the lateral teeth they are relatively short and moderately straight and are increasingly strongly produced and flange-like towards their postero-lateral extremities where they are abruptly truncated.

The median part of the labrum (Figs 26 and 28) is only weakly raised above the level of the lateral wings and is also only weakly concavely dished whereas in *A. mutilloides* the median part of the labrum (Figs 25 and 27) is both strongly raised and strongly concavely dished.

Male Unkown.

Material examined: Transvaal; Carolina, 13.i.1917 (G. A. H. Bedford) Holotype ♀ (South African Museum ex National Museum Bulawayo 1981); Pretoria, 24.x.1914 (no collector) Paratype ♀ (South African Museum ex National Museum Bulawayo 1981); Rustenb[urg], iii. [18] 85 (L. Schunck) Paratype ♀ (South African Museum ex National Museum Bulawayo 1981) (bearing two additional labels: 127; *Ampulex/ mutilloides/* Kohl ♀/ determ/ Dr. Brauns); Ermelo, 21.xi.1948 (N. C. Mokhehle) Paratype ♀ (Albany Museum).

Etymology: The name *timulloides*, suggested to the author by his colleague, the late Mr C. F. Jacot-Guillarmod, is an anagram of *mutilloides* and thereby draws attention to the similarity shown by these two species.

KEY TO FEMALES OF SOUTHERN AFRICAN SPECIES OF *AMPULEX* IN WHICH THE PRONOTUM IS NOT POSTERIORLY RAISED INTO A CONICAL TUBERCLE

The genus *Ampulex* may for convenience be divided into those species in which the pronotal collar is posteriorly raised into a conical tubercle and those in which such a conical tubercle is lacking. Of the 42 species of *Ampulex* listed for the Afrotropical Region by Bohart and Menke (1976: 77–78) at least 12 species belong to the tubercle-less group. To their number may be added the five species here described as new.

The present key dealing with the tubercle-less group is limited to those species occurring in southern Africa. It is further limited to the females for, as only one of the newly described species, *bantuae*, is known from both sexes, little could be added to the key to males given by Arnold (1928). In accordance with these restrictions the following species have been omitted: *honesta* Kohl and *splendidula* Kohl, both described from females and known respectively from Gabon and Zaire and from central Africa; *overlaeti* Leclercq and *pilipes* Kohl, both described from males and known respectively from Zaire and from Guinea and Mozambique. *A. chalybea* Smith, described from a female from an unspecified part of Africa, is omitted as the description is entirely inadequate.

1. Pronotal collar without a conical tubercle behind 2
— Pronotal collar with a conical tubercle behind .... See Arnold (1928: 200)
2. Pronotal collar with two transversely placed small, low and blunt teeth at about or a little behind middle; body black, without metallic lustre (Forewing with two cubital cells) 3
— Pronotal collar unarmed; body with at least some metallic lustre (blue, green or purple) 4
3. Legs with coxae and femora fusco-ferruginous and tibiae and tarsi ferruginous (occasionally legs are entirely ferruginous); abdomen dull, microscopically reticulate-punctate (Cape Province, Natal, Swaziland, Transvaal and Zimbabwe) .... **denticollis** Cameron
— Legs with coxae, femora and tibiae black and last three tarsal segments brownish-black; abdomen smooth and shining, second tergite with a few very small scattered punctures (Malawi, Mozambique and Urundi) .... **lugubris** Arnold
4. Head (to a varying degree), pronotal collar, scutum and scutellum bright ferruginous and without metallic lustre 5
— Head, pronotal collar, scutum and scutellum without ferruginous colour 6
5. Head width across eyes equal to or slightly less than length from anterior margin of scutum to brink of propodeal declivity measured along dorsal midline (see Fig. 30); vertex and occiput with close and coarse punctures separated by rugae; lateral wings of clypeus (Figs 23 and 25) well developed and produced and anteriorly separated from lateral teeth; median part of labrum (Figs 25 and 27) strongly raised above lateral wings and strongly concavely dished (Cape Province, Lesotho, Natal and Zimbabwe) .... **mutilloides** Kohl
— Head width across eyes exceeding by a mean factor of 1,14 length from anterior margin of scutum to brink of propodeal declivity measured along dorsal midline (see Fig. 30); vertex and occiput with widely spaced, large and deep punctures, the spaces between them smooth and shining; lateral wings of clypeus (Figs 24 and 26) poorly developed and receding, anteriorly not separated from lateral teeth; median part of labrum (Figs 26 and 28) only weakly raised above lateral wings and only weakly concavely dished (Transvaal) .... **timulloides** sp. nov.
6. Clypeus produced into a broad, subquadrangular and transversely convex plate, not carinate longitudinally in middle and without a median tooth on anterior margin; fun-

damental sculpture on head and pro-mesonotum exceedingly fine, consisting of a microscopic and very close puncturation, so that those parts are dull; fourth carina of epinotal dorsum obsolete. (Forewing with two cubital cells.) Small species, 8 mm long (Griqualand West and Zimbabwe) .... ***arnoldi*** Brauns

— Clypeus differently formed, tectiform or nasiform, carinate longitudinally in middle, carina ending on anterior margin in a distinct tooth or on a wide, subtruncate lobe (*bantuae*) 7

7. Clypeus (Figs 2 and 9) nasiform; lateral wings of clypeus poorly developed and like lateral teeth downwardly directed and thus appearing to be strongly receding when seen from above; labrum (Fig. 14) triangular in overall shape, greatly but regularly widened from base to apex and with extensive lateral wings exceeding median part; frontal lobes (Fig. 2) arcuately expanded laterally and completely covering antennal sockets; frontal carinae parenthesis-like (Cape Province) .... ***bantua*** sp. nov.

— Clypeus (Figs 1, 3, 4 and 5) tectiform; lateral wings of clypeus well developed and like lateral teeth antero-laterally directed; labrum (Figs 13, 15, 16 and 17) differently formed, with median part greatly produced and by far exceeding strongly down-curved lateral wings which flank it basally; frontal lobes (Figs 1, 3, 4 and 5) not arcuately expanded laterally and not covering antennal sockets; frontal carinae diverging posteriorly 8

8. Lateral wings of clypeus extending postero-laterally without interruption and without emargination entire distance to mandibular sockets (Fig. 5); forewings with a tendency towards loss of first intersubmarginal veinlet leading to frequent coalescence of first and second submarginal cells; (head, thorax and legs with sparse, very coarse black pilosity) 9

— Lateral wings of clypeus not extending postero-laterally without interruption but terminated abruptly and separated from mandibular sockets by an emargination (Figs 1, 3 and 4); forewings not showing this tendency and therefore always with three submarginal cells 10

9. Claws of all legs bifid (inner ramus of claws apically pointed, wider than outer ramus and only slightly shorter); body metallic blue and green, last three tergites and apical half of third, last four sternites, clypeus, mandibles, scapes and pedicels ferruginous (Cape Province and Natal) .... ***apicalis*** Smith

— Claws of all legs toothed (tooth acutely pointed, situated midway along length of claw and at right angles to it); body metallic blue (sometimes abdomen is lustreless black) with only mandibles and antennal scapes ferruginous (Cape Province) .... ***nigrisetosa*** sp. nov.

10. Small species, 7,5 mm or less in length (mandibles, apex of clypeus, antennae, apical segment of abdomen, legs various shades of brown; wings hyaline, forewing with a transverse fuscous band) (Cape Province) .... ***nebulosa*** Smith

— Larger species, 10–16 mm in length 11

11. Labrum (Figs 10 and 15) with median part more or less square in cross-section, in dorsal view with sides subparallel and with apical margin pointedly bilobed, with apical face concave and ventral face flat; wings strongly and fairly uniformly browned, without noticeable fasciae; (frontal lobes very strongly raised laterally; frontal carinae strongly divergent posteriorly; puncturation of head and thorax coarse) (Lesotho) .... ***lesothoensis*** sp. nov.

— Labrum (Figs 8 and 13; 11 and 16) with median part flattened, in dorsal view with sides diverging anteriorly and with anterior margin widely bilobed and slightly down-curved, with ventral face concave; wings subhyaline, lightly browned, with fasciae (*cyanura*) or without fasciae (*montivaga*) 12

12. Mandibles black (except for tips), other than for absence of metallic lustre not contrasting with colouration of genae (mountains of Lesotho) .... ***montivaga*** sp. nov.
— Mandibles ferruginous, contrasting markedly with colouration of genae 13
13. Mandibles in lateral view with a pronounced bluntly triangular lamelliform projection of lower edge (Fig. 18); punctures of first two tergites shallow, fine to moderate in size 14
— Mandibles in lateral view with only a very low lamelliform projection of lower edge; punctures of first two tergites deep, very distinct, moderate in size; clypeus ferruginous (mountains of eastern Zimbabwe) .... ***cyanura monticola*** Arnold
14. Clypeus, scapes and frontal lobes black (Cape Province and Zululand) ....
.... ***cyanura cyanura*** Kohl
— Clypeus, scapes and anterior portions of frontal lobes ferruginous (Zimbabwe) ......
.... ***cyanura rhodesiana*** Arnold

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The author wishes to thank Dr F. Koch of the Museum für Naturkunde an der Humboldt-Universität zu Berlin and Mr M. C. Day of the British Museum (Natural History), London, for making it possible for him to examine the holotype of *Ampulex cyanura* Kohl.

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Some aspects of the ethology of *Ampulex bantuae* Gess (Hymenoptera: Sphecidae: Ampulicinae) in the Eastern Cape Province of South Africa

by

F. W. GESS

(Albany Museum, Grahamstown)

CONTENTS

ABSTRACT

Some aspects of the ethology of *Ampulex bantuae* Gess (Hymenoptera: Sphecidae: Ampulicinae) in the Eastern Cape Province of South Africa are described. Particular attention is paid to: the situation and nature of the nest; the identification and biology of the prey; prey selection; the hunting, stinging, malaxation and conveyance of the prey to the nesting cavity; the positioning of the prey within the nesting cavity, oviposition and nest closure; life history, voltinism, mating, longevity and fecundity. A definite relationship between the size of the prey and the sex of the wasp which develops upon it is demonstrated.

Some aspects of the hunting and nesting behaviour of nine *Ampulex* species are briefly reviewed. It is found that the nesting behaviour of *A. bantuae* does not differ to any significant extent from that of these species and it is concluded that the ethology of *Ampulex* is characterized by marked interspecific uniformity. Various adaptations which enable *Ampulex* to lead an arboreal life are discussed.

INTRODUCTION

A very brief outline of some aspects of the ethology of *Ampulex bantuae* Gess (as *Ampulex* sp. near *cyanura* Kohl) and a discussion of its role within a community of insects has previously been published as part of a general ethological study of the aculeate wasps and the bees of a karroid area in the vicinity of Grahamstown, South Africa (Gess, 1981: 29 and 72–75, Figs 34–36).

The present publication deals in greater detail with those aspects of the ethology which were previously merely outlined and furthermore introduces other aspects which were omitted from the earlier publication as not relevant to its subject.

Ampulex bantuae is a medium-sized, metallic-blue wasp not often seen in the field and consequently little known and poorly represented in collections. However, it proved that the species' rarity in the field is apparent rather than real and that the impression of rarity is largely due to the wasp's clandestine life history. At the site of the study *A. bantuae* is a not uncommon insect within its restricted habitat.

The present study resulted from the utilization for nesting purposes by *A. bantuae* of trap-nests of the type described by Krombein (1970) placed in the field during the summers of 1973–74, 1974–75, 1975–76 and 1976–77. In consequence of the discovery that *A. bantuae* nested only in those trap-nests suspended within *Acacia karroo* shrubs and trees, a close examination of these was undertaken, which in turn led to the exciting unfolding of the particulars of the nesting of *A. bantuae* under natural conditions.

The hunting and nesting behaviour of *A. bantuae* is such that the physical requirements necessary for the normal performance of these activities can readily be provided in the laboratory. This made it possible in the present study to observe the behaviour of captive individuals and to carry out some experiments which would have been impossible with free wasps in the field.

The present paper is the fourteenth in a series of publications dealing with the ethology of certain solitary wasps occurring at Hilton, a farm situated 18 kilometres WNW of Grahamstown (33° 19′S, 26° 32′E) in the Albany Division of the Eastern Cape Province of South Africa. A detailed account of various aspects of the ecology of Hilton has previously been given (Gess, 1981: 3–9).

DESCRIPTION OF THE NESTING SITES

The natural nesting sites of *A. bantuae* at Hilton are the disused galleries of *Ceroplesis hottentota* (Fabr.) (Cerambycidae). The larvae of *C. hottentota* in the course of their feeding bore galleries in finger-thick terminal branches of *A. karroo.* After they have completed their larval feeding, have pupated and have metamorphosed into adults, the beetles break out and abandon their galleries with the result that the latter become available for the use of other insects which cannot themselves hollow out such cavities.

The natural nests of *A. bantuae* were discovered as a result of making a survey of trap-nesting wasps and bees at Hilton. *A. bantuae* nested only in those trap-nests hung in *A. karroo* and then only in a restricted area (Fig. 1). This led to a closer examination of these shrubs or small trees.

The trap-nests utilized by *A. bantuae* were of the type described by Krombein (1970). Borings of three sizes, 6,4 mm, 9,5 mm and 12,7 mm, were offered but only those of the two smaller sizes were utilized. These trap-nests were suspended from horizontal living branches at heights between 10 cm and 200 cm above the ground.

Fig. 1. Hilton, iv.1974. One of a scattering of small *Acacia karroo* trees in which were hung trap-nests which were utilized by *Ampulex bantuae*.

IDENTIFICATION, DISTRIBUTION AND BIOLOGY OF THE PREY

At Hilton, *A. bantuae* was found to provision its cells with a single species of cockroach, *Bantua dispar* (Burmeister) (Blattariae: Derocalymmidae), one of four species of the genus *Bantua* Shelford endemic to southern Africa. *B. dispar* appears to be restricted in its distribution to the south-eastern parts of the Cape Province. Princis (1963: 130) recorded the species from Grahamstown (the type locality), Resolution (18 km NNE of Grahamstown), Great Fish River (48 km E of Grahamstown), Port Elizabeth, Dunbrody and Willowmore. Specimens in the Albany Museum collection are from several localities around Grahamstown.

Adult males of *B. dispar* are fully winged whereas females are totally apterous. Male and female nymphs are similar in appearance but may readily be distinguished in all instars by differences in the form of the terminal abdominal sternites.

At Hilton *B. dispar* was found to be restricted to *Acacia karroo* where during the day it hides under loose bark or in old galleries of *Ceroplesis hottentota.* Both the nymphs and the adults were very commonly found sheltering in trap-nests suspended from branches of *A. karroo*. Individuals kept in captivity spent the day in hiding in dark places but came out at night when they fed eagerly upon *A. karroo* gum which had been placed in the cages. It is believed that it is this gum, which exudes copiously from any injuries to the bark including those caused by the activities of *C. hottentota,* that constitutes the natural food of *B. dispar* and that the restriction of the cockroach to *A. karroo* is due to this food preference.

DESCRIPTION OF THE NEST

The nest of *A. bantuae* is single-celled. The only building material added to the pre-existing cavity is debris used for constructing the cell closure. No preliminary plug and no closure to the gallery opening are constructed.

Thirteen natural nests were found. Thirty-six nests constructed in trap-nests in the field were obtained, twenty-four were in 6,4 mm borings and twelve in 9,5 mm borings. An additional fifty-four nests were constructed in trap-nests by captive females.

Due to the fact that the loosely-packed nest closures were displaced on splitting open the hollowed out *A. karroo* branches, no accurate measurements were obtained from natural nests. In trap-nests from the field, nests consisting of the cell and its closure were 43–145 mm long with a mean length of 97 mm in the 6,4 mm borings, and 54–77 mm long with a mean length of 63 mm in the 9,5 mm borings. The closures were 16–83 mm long with a mean length of 36 mm in the 6,4 mm borings, and 27–41 mm long with a mean length of 35 mm in the 9,5 mm borings.

The materials comprising the closures were loosely compacted and consisted of a mixture of various kinds of detritus collected by the wasp on or beneath the *Acacia karroo* shrub or tree from which the trap-nest was suspended. The materials utilized in natural nests and in trap-nests in the field consisted in order of frequency of use of: small pieces of *A. karroo* bark, sometimes lichen covered; *A. karroo* leaflets, mostly dry; faecal pellets of caterpillars; fragments of insect exo-skeletons, including the pronotal shield of *B. dispar* and an elytron of *C. hottentota*; the exuviae of *B. dispar*; small twigs; *A. karroo* inflorescences, both fresh and dry; *A. karroo* seeds; a length of dry grass leaf blade; a dried-out tick; rodent droppings and fragments of dung of larger mammals; a live lepidopterous pupa (Limacodidae). It appears that any available detritus is utilized for constructing the closures. Wasps nesting in captivity took small rounded quartzite pebbles if no other materials were provided.

NESTING

Prey selection

The prey of *A. bantuae, Bantua dispar*, is a hemimetabolous insect. All stages, from freshly hatched first-instar nymphs to adults of both sexes therefore occur together upon *Acacia karroo* and are met with by the wasp during the course of her hunting.

Like all species of *Ampulex, A. bantuae* provisions each of her cells with but a single cockroach. As this has to provide all the nutritional requirements of the wasp larva which will feed upon it, it must clearly be selected by the wasp to satisfy certain physical parameters. These could to a large degree be established from prey found in natural nests and in trap-nests at Hilton and from the study of the response by captive female wasps to cockroaches differing in size, age and sex.

Forty-two cockroaches utilized as prey in natural nests and in trap-nests at Hilton were examined. Their lengths varied from 15–22 mm. The majority, thirty-seven, were females, both nymphs and adults, with lengths ranging from 17–22 mm and averaging 20,2 mm. The remainder, five, were male nymphs with lengths of 15, 17, 18 and 19 (two) mm. No adult (winged) males were represented amongst the prey.

Given cockroaches of both sexes and a range of sizes, captive *A. bantuae* females showed prey preferences similar to those established for free females. Fifty-eight cockroaches were taken as prey. The majority, forty-eight, were female nymphs and adults ranging in length from 13,0–23,3 mm (average 19,3 mm). The remainder, ten, were male nymphs ranging in length from 14,7–19,7 mm (average 18 mm). As in the sample from field nests no adult (winged) males were represented amongst the prey.

Nymphs at the extreme lower end of the size range were taken only when larger cockroaches were withheld. The smallest nymph taken, a female of 13,0 mm, was stung and transported to a nesting cavity but was abandoned there prior to oviposition. The smallest prey to be oviposited upon was a slightly larger nymph, a female of 13,5 mm, from which a very small

male wasp was successfully reared. Wasps could not be induced to take adult (winged) males even when confined with them in the absence of wingless cockroaches.

It is apparent from the above that there are two criteria which individuals of *B. dispar* have to fulfil in order to be acceptable as prey: they must be larger than a certain minimum size (*c.* 13,5 mm long) and they must be apterous.

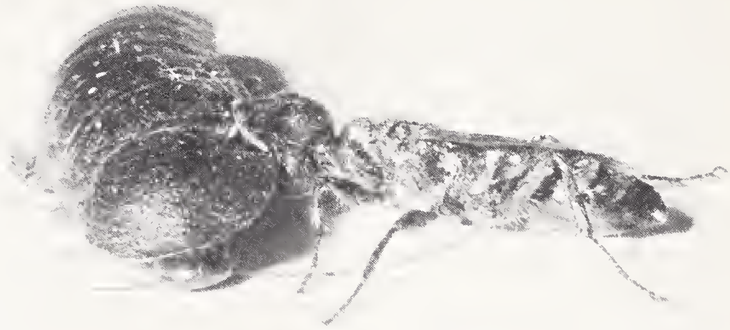
The wasp's acceptance as prey of larger male nymphs, including those in the last nymphal instar, but its consistent rejection of adult males indicates its reaction to some character exhibited by the adult male cockroach. Whether this character is merely a morphological one (such as the presence of wings), a behavioural one depending upon the presence of wings (such as the male cockroach's habit of stridulating when it is inspected by a wasp), or a chemical one (such as the possession of a pheromone) was not established. However, whatever the means by which the wasp recognises an adult male, its rejection of the latter as prey is of survival value as it would represent a deficient investment in terms of the amount of food it could provide for a wasp larva developing upon it. It was found that for female nymphs and adults and male nymphs (including those in the last nymphal instar) there is a directly proportional relationship between body length and body weight which is common to all three categories. Adult (winged) males, however, have a weight which is less than their body length would suggest on the basis of the above weight/length relationship. Thus the weight of adult male cockroaches was found to be only about 67% of the weight of male and female nymphs of the same body length. The loss in weight at the time of the final moult results in the adult winged male having a weight below that found necessary for successful development of wasp larvae upon wingless male nymphs and female nymphs and adults. Adult males are therefore unsuitable for the same basic reason as are nymphs below a minimum size.

As stated in the previous section *A. bantuae* at Hilton restricts its choice of prey to *Bantua dispar* (Derocalymmidae) which it also readily takes in captivity. In order to establish whether *A. bantuae* is indeed species-specific with respect to its prey, two cockroaches of other species were offered to captive females. Both met the requirements with respect to body length, body weight and winglessness established for the acceptance by the wasp of individuals of *B. dispar*. The first, an adult female *Pseudoderopeltis* sp. (Blattidae) was confined with a female wasp for a period of sixteen days, during the first four days in company with three *B. dispar* and during the last two days in company with one *B. dispar*. All four *B. dispar* were taken as prey but the *Pseudoderopeltis* sp. was not in any way molested and during the period laid two oothecae. The second, a female, nymph of *?Perisphaeria* sp. (Perisphaeriidae) was confined with three female wasps for a period of eleven days and was similarly left unmolested though five *B. dispar* introduced into the cage during the period were all taken. The species specificity seen in the field with regard to the prey taken was therefore confirmed in the laboratory.

Hunting, grasping and stinging, malaxation and conveyance of the prey to the nesting cavity

Hunting is done on foot, the wasp moving hurriedly but by fits and starts, twitching the wings which are held folded over her back. Very noticeable are the antennae which are held out in front of the head and curve out to the sides and which are kept in constant motion, seemingly 'drumming' the surface on which the wasp is walking. Close observation of the rapidly moving antennae leads to the conclusion that each antenna as a whole is actually describing an elliptical path, the direction of movement of one being clockwise, that of the other anticlockwise. Together they are brought down towards the surface, move inwards towards each other, are raised up and move apart. At the same time the abdomen is continually moved up and down and is also frequently moved in and out telescopically.

A suitable cockroach having been located and, if attempting to escape, pursued, the wasp advances upon it with widely separated mandibles and having positioned herself favourably lunges forward and seizes it by the anterior, antero-lateral or lateral margin of the pronotal



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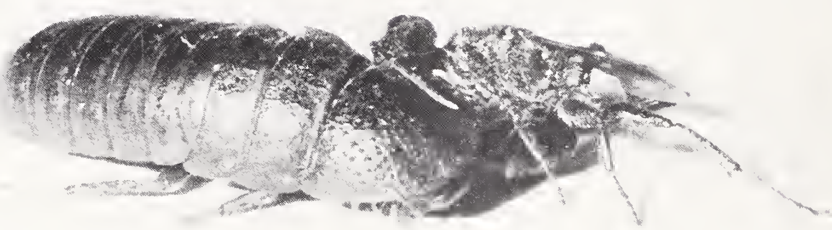

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Figs 2 and 3. Female *Ampulex bantuae* holding a female *Bantua dispar* by pronotal shield subsequent to initial stinging (Fig. 2) and flexing abdomen beneath same to administer additional sting (Fig. 3). (Both ×4,25)

shield, one mandible being positioned on the upper surface of the pronotal shield, the other on the lower surface, the wasp's head being held sideways. The wasp then flexes her abdomen downwards and forwards between its wide-spread legs to bring the tip of the abdomen, which is seen to extend telescopically, into position on the underside of the prey, the wasp all the time retaining her hold on the pronotal shield. Probing with the tip of the abdomen in the neck region and between the legs then takes place. In one observed case several stings appeared to be given to the prey, the last being between the prothoracic legs or in the neck region. In another case it appeared that only one sting in the neck region was given. The probing and stinging may take five or more minutes. After the initial stinging the wasp may once or twice straighten her abdomen, pull the cockroach into a slightly different position and again flex the abdomen into the stinging position (Figs 2 and 3).

The cockroach having been stung it immediately stops struggling and lies still, its legs unable to support its weight. The wasp straightens her abdomen and ceases the antennal 'drumming' which had been carried on during the stinging and handling of the cockroach. The wasp then usually relinquishes her hold of the prey and withdraws to a short distance where she commences grooming.

In grooming, the antennae are cleaned with the fore-legs and the abdomen on its dorsal surface and its sides by the hind-legs. The fore- and middle-legs of each side are rubbed against each other and the hind-legs are rubbed one against the other and also together against one of the middle-legs.

The cockroach appears to recover gradually from the initial collapse caused by the stinging and stands up, feebly supporting its weight on its legs. It may do a small amount of grooming and has been seen to raise the thorax on one side and to try with its mouthparts to reach the sting sites on the underside of the thorax.

Whilst the cockroach is recovering, the wasp inspects it from time to time. As before, she holds it by the pronotal shield and in addition sometimes tugs it in the direction of the cavity in which nesting is to take place. When the cockroach is sufficiently recovered to stand, the wasp reaches with her head and mandibles beneath the pronotal shield covering the cockroach's head and takes hold of and draws out forwards one of the antennae (Figs 4, 5 and 6). Taking hold of this antenna near its base the wasp then proceeds to walk backwards leading the cockroach towards the nesting cavity. The cockroach at the end of its antennal 'leash' walks forwards following the wasp and makes no attempt to resist or to escape even when the wasp occasionally releases her hold in order to run off to inspect the nesting cavity and the way to it. On returning to the cockroach the wasp once again reaches under the pronotal shield in order to grasp the antenna.

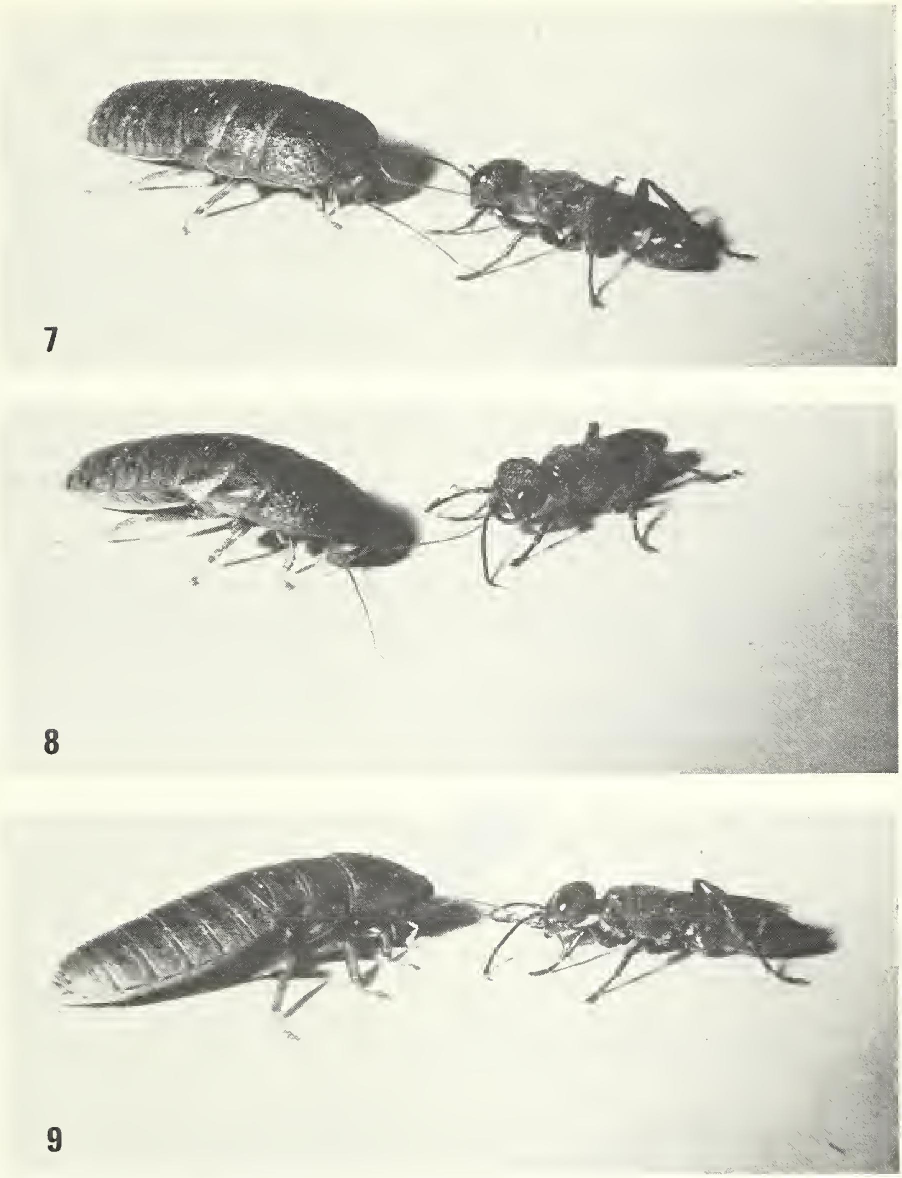
Occasionally a wasp does not lead away her prey immediately upon first grasping the antenna but rather passes the antenna through between her jaws until a point near the end is reached when the jaws tighten their grip and the wasp proceeds vigorously to pull and tug at the antenna which can be seen to be pulled taut (Fig. 7). The tugging is accompanied by wing buzzing on the part of the wasp and a short length of antenna, the distal five segments or so, is severed and discarded. The wasp retains the end of the antenna between her mouthparts for some time and it appears as if, at this juncture, blood is being imbibed by the wasp from the now slackly held antenna (Figs 8 and 9). While she is imbibing blood the wasp may groom her abdomen and legs. Occasionally both antennae are severed. Therefore it appears that at least in some cases the wasp imbibes blood oozing from a wound or wounds deliberately inflicted upon the prey for this purpose. It is noteworthy that the reaction of the stung cockroach to antenna-pulling varies according to where the antenna is grasped. Whereas the cockroach walks forwards when grasped near the base of the antenna as is the case during its conveyance to the nesting cavity, it stands firm when grasped near the tip of the antenna. This behaviour enables the wasp after some effort to pull off the distal segments.

4

5

6

Figs 4–6. Female *Ampulex bantuae* reaching beneath pronotal shield of a stung female *Bantua dispar* to take hold of an antenna (Figs 4 and 5) and drawing out the same (Fig. 6). (All ×2,5)



Figs 7–9. Female *Ampulex bantuae* pulling taut an antenna of a stung female *Bantua dispar* prior to severing its distal portion (Fig. 7) and imbibing blood from the cut end of the now slackly held antenna (Figs 8 and 9). Note the severed distal portion of the antenna at bottom right-hand corner of Fig. 9. (All ×2,5)

Positioning of the prey within the nesting cavity, oviposition and nest closure

On arrival at the nesting cavity the wasp enters it backwards and continues backing in until she reaches the inner end, all the while drawing the cockroach in after her so that it comes to face the blind end of the cavity. Oviposition upon the prey then takes place. For this a very characteristic posture relative to her prey is assumed by the wasp, still positioned at the cockroach's head end. In the case of a cockroach lying on its left side, the wasp's right mandible grips the dorsal surface of the pronotal shield and the left mandible the ventral surface of the pronotal shield and the head. The wasp's left antenna lies dorsally along the ridge of the pronotal shield on the right side and extends as far as the angle of the ridge at the hind end of the shield. The anterior edge of the pronotal shield is situated between the wasp's antennal bases and at the base of the clypeus. The wasp's meso- and metathoracic legs extend backwards towards the blind end of the nesting cavity, its abdomen is flexed downwards and forwards and extends under the left side of the cockroach with the tip near the base of a metathoracic leg where the egg is attached.

In a sample of fifty prey cockroaches in trap-nests for which all the necessary details were noted, it was found that there was a random relationship between the number of cockroaches positioned in the cell to lie on their left sides and those positioned on their right sides; similarly that there was a random relationship between the number of times eggs were laid on one side or the other. However, it was found that eggs were more than twice as likely to be laid on the side on which the cockroach was lying than on the opposite side.

The egg is cemented over its entire length to the underside of the cockroach and is orientated obliquely at an angle of between 35° and 40° to the long axis of the prey. The egg's posterior half is situated upon the basal half of the flattened antero-ventral surface of the metathoracic coxa and its anterior half is on the adjoining metathoracic trochantin to which the coxa is articulated (Fig. 10). In only one of the sixty-eight instances in which its position was

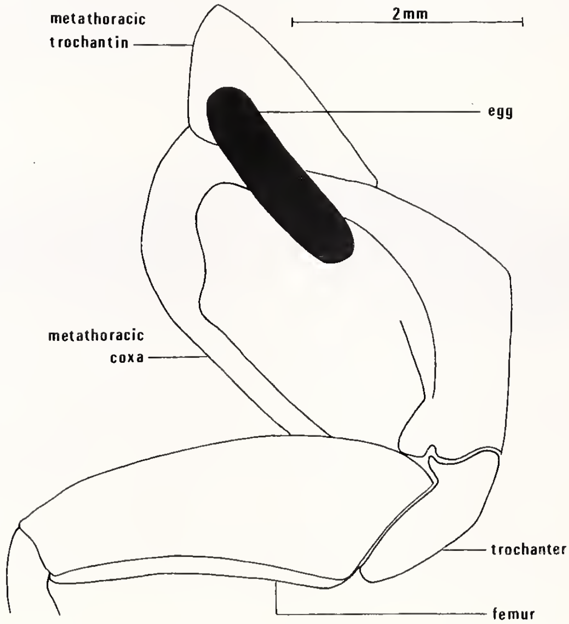


Fig. 10. Diagrammatic representation of the ventral surface of the base of the right metathoracic leg of a female *Bantua dispar* showing the positioning upon it of an egg of *Ampulex bantuae*.

noted was an egg found situated elsewhere. In this instance it occupied the same position on the coxa and trochantin but the leg involved was that of the mesothorax as opposed to that of the metathorax. The egg did not develop.

Oviposition completed, the wasp squeezes past the cockroach and emerges from the nest. Collection of detritus for the sealing of the nesting cavity is thereafter undertaken. Each piece of detritus, held with the mandibles, is carried to the cavity on foot.

In captivity in a glass-sided cage with a floor area of 30 cm x 60 cm and furnished with trap-nests and detritus suitable for nest closure it was found that about $2\frac{1}{2}$ hours elapsed between the first contact of the wasp with its prey and the completion of the nesting cavity closure following oviposition.

LIFE HISTORY, VOLTINISM, MATING, LONGEVITY AND FECUNDITY

Eighty-eight of the 100 cockroaches obtained from *A. bantuae* nests bore viable eggs. Sixty of the young wasp larvae which hatched from these eggs were successfully reared through to the adult stage. The remaining twenty-eight individuals died at various times during their development. For all individuals the dates on which major developmental events occurred were recorded.

The egg is off-white and slightly curved. A total of sixteen was measured. All were very similar in size, the average length and the average diameter at the middle being 2,04 and 0,54 mm respectively.

The time from oviposition to egg hatch is three to nine days, most commonly five. Larval feeding commences very close to the position of the anterior end of the egg, namely at the weakly sclerotized antero-lateral margin of the trochantin and continues at this point for a period of four to eleven days. During this time the larva moults but retains a position very similar to that previously occupied by the egg. The larva as it grows covers most of the trochantin and the flattened antero-ventral face of the coxa, its posterior end fitting into the angle formed by the distal part of the coxa and the proximal part of the femur. When the larva has attained a length of about 4,5 mm it migrates from the exterior feeding position through the hole created during feeding to within the body of the still living cockroach, disappearing from view. The egg pellicle and the larval exuviae are left adhering to the coxa and trochantin. The larva continues feeding within the cockroach which dies two to six, most commonly three, days after larval entry.

The presence of the *A. bantuae* larva within the cockroach causes its body to be slightly arched, its sternites to be noticeably curved and its legs frequently to be somewhat raised and held away from its body (Fig. 11). After the death of the cockroach its exo-skeleton dries in this configuration and in the field dead cockroaches containing *A. bantuae* are fairly easy to recognize on this account,

The mature *A. bantuae* larva, having eaten out all the soft tissues inside the cockroach, remains within the now empty but perfectly intact body shell within which it subsequently spins its cocoon and pupates.

The cocoon is brown, smooth, shiny, hard and brittle and is terminated at each end by a pronounced nipple-like projection. This hard cocoon is contained within an envelope of off-white spinnings which are adpressed to the inside of the cockroach's exo-skeleton over most of the length of the cocoon but are more loosely arranged at the cocoon's two ends where they are also most plentiful. The hard cocoon almost entirely fills the available space within the cockroach. For example, a cocoon which was 11,3 mm long and had a maximum width at the middle of 3,8 mm was accommodated within the body of a cockroach the external length of which was 15 mm.

That the anterior end of the cocoon was directed towards the anal end of the cockroach

Fig. 11. Female *Bantua dispar* showing typical body configuration associated with the presence within it of a feeding *Ampulex bantuae* larva. (×1,9)

Fig. 12. Hollowed out exo-skeleton of female *Bantua dispar* with apical segments of abdomen and exposed end of *Ampulex bantuae* cocoon removed to show orientation of wasp pupa. (×1,9)

Fig. 13. Hollowed out exo-skeleton of female *Bantua dispar* with female *Ampulex bantuae* which emerged from it. The anterior end of the wasp's cocoon is visible within the apical segments of the cockroach's abdomen cut off by the emerging wasp. (×1,9)

was established by breaking off the last few abdominal segments of two cockroaches and carefully removing the exposed ends of the *A. bantuae* cocoons within. Each cocoon contained a pre-pupa facing the opened end—that is the posterior end of the cockroach. Pupation occurred within a few days. In both instances the pupae were so positioned that they were the same way up as the cockroach—that is the dorsal surface of the *A. bantuae* pupa was against the dorsal surface of the cockroach (Fig. 12). The adult *A. bantuae* emerges by cutting off first the end of its cocoon and then the end of the cockroach's abdomen (Fig. 13). As the cockroach is always positioned within the cell facing the inner or blind end of the nesting cavity the *A. bantuae* within the cockroach is not only facing the correct way for emerging easily from the latter but is also facing the outer end of the cell and has only to pass through the detritus plug before emerging into the open.

A. bantuae at Hilton is bivoltine and proterandrous. Developmental times for thirty-eight individuals reared during the period from November, 1973 to January, 1975 are plotted in Fig. 14. Developmental times established during other years were found to be very similar. During 1973–74 the first or summer generation resulting from eggs laid in trap-nests in the field during November and December, 1973 developed rapidly. Males emerged from mid January to the end of February, 1974 and females from late January to the end of the first third of March, 1974. Developmental periods from oviposition to adult emergence were about sixty-three days for males and about seventy days for females.

The second or overwintering generation resulting from eggs laid in trap-nests in the field and in the laboratory during February and March, 1974 underwent a pre-pupal diapause as shown by the presence of pre-pupae in cocoons opened during early November, 1974. These pre-pupae changed to pupae within one to a few days following cocoon opening. Males of this generation emerged during the first half of December, 1974 and females from mid December,

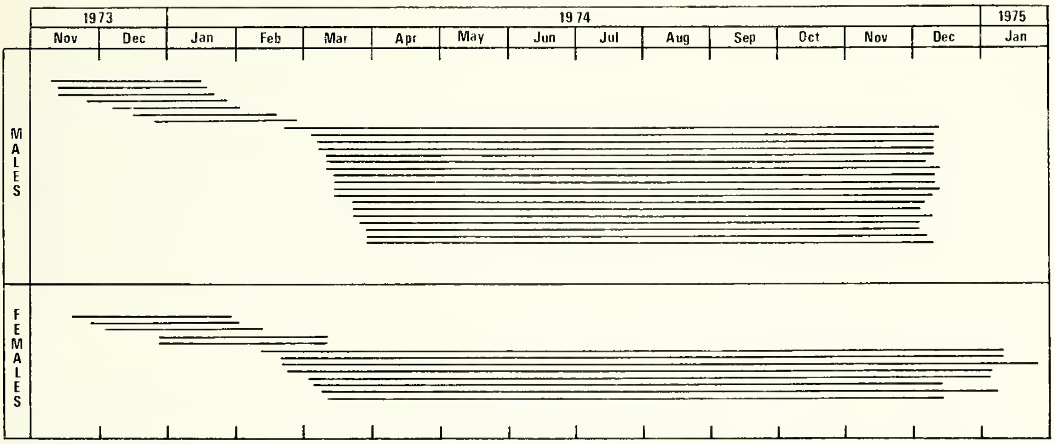


Fig. 14. Developmental times for 38 individuals (25♂♂ and 13 ♀♀) of *Ampulex bantuae* reared during the period from November, 1973 to January, 1975. That *A. bantuae* is bivoltine is shown clearly.

1974 up to mid or even late January, 1975. Developmental periods from oviposition to adult emergence for second generation wasps ranged from 251–295 days for males and from 276–340 days for females. These developmental periods for second generation wasps of both sexes are clearly unnaturally long. Instead of emerging during December–January as here recorded this generation under natural conditions probably emerges during late October–early November in order that first generation eggs of the following summer season may be laid later in the latter month. The cause for the protracted developmental periods of the second generation wasps may be ascribed to the fact that the trap-nests containing the diapausing wasps were kept indoors and were therefore not subjected to the temperature and humidity conditions prevailing in the field. The same phenomenon has been found with respect to developmental periods of diapausing *Isodontia pelopoeiformis* (Dahlbom) (Gess and Gess, 1982).

It has been shown that wasps of the non-diapausing first generation take a fixed number of days to develop from egg to adult. The wasps of the diapausing second generation, however, show no such fixed time period for their development. Irrespective of how early or how late the second generation eggs are laid, the development of all the individuals hatching from them is held up at the pre-pupal stage during the autumn, winter and spring months. Further development of all takes place when diapause is broken in early summer and the long delayed moult from pre-pupa to pupa takes place. Post-diapause developmental times differ between males and females for the second generation of wasps, like the first, is proterandrous.

Mating in captivity was observed in two instances. The wasps involved were all newly emerged, the males having emerged three to ten days and the females one to two days previous to their being introduced together into a cage. In both cases the males ran about the floor of the cage in great agitation apparently searching for a female. After five to ten minutes, a female having been located, the male immediately mounted her, there being no preliminary courtship. She extruded her genitalia and fusion of the genitalia took place. The male then dismounted and the two wasps assumed a tail-to-tail attitude, facing in opposite directions. One pair separated after fifty seconds in this tail-to-tail attitude. The total time taken for copulation was in one instance one minute and in the other two minutes. After separation the male groomed extensively.

Little was established concerning the longevity and fecundity of *A. bantuae*. However, some indication will be gained from a consideration of five females kept in captivity. Two were captured as adults. The first, captured in the field at Hilton on 25.ii.1974 just after ovipositing on a cockroach in a trap-nest, laid a total of thirteen eggs during the following thirty-six days. She died after forty-three days in captivity. The second, captured at Hilton on 15.iii.1974 after ovipositing on a cockroach in a natural nest, laid a total of four eggs during the following twenty-seven days. She died after forty-one days in captivity. The remaining three females emerged in captivity. The first emerged on 28.ii.1974 from a dead cockroach found in a natural nest. During her adult life of forty-four days she laid a total of eleven eggs. The second emerged on 10.iii.1974 from a trap-nest. During her adult life of eighteen days she laid two eggs. The third emerged on 11.iii.1974 from a trap-nest. During her adult life of forty-nine days she laid three eggs. With respect to all five females more eggs might have been laid had the supply of cockroaches not sometimes failed.

SEX OF WASP IN RELATION TO SIZE OF PREY UPON WHICH IT DEVELOPED

In the section dealing with prey selection by *A. bantuae* an account has been given of the preferred size range of cockroach prey. It was also shown that, as the prey has to be apterous, nymphs of both sexes and also adult females are taken but that adult males which are winged are rejected. Whether the size of the prey has any bearing upon the sex of the wasp which develops upon it will now be considered.

Forty-nine *A. bantuae*, twenty-four males and twenty-five females, were reared on cockroaches ranging in length from 15–23 mm. The differences in the frequency of utilization of different length categories (grouped to the nearest mm) of the cockroach for rearing males and females are shown graphically in Fig. 15. It can be seen that the majority, twenty-one, of the males were reared on cockroaches up to 20 mm in length and the majority, nineteen, of females were reared on cockroaches of 20 mm or more in length. Prey size does therefore have

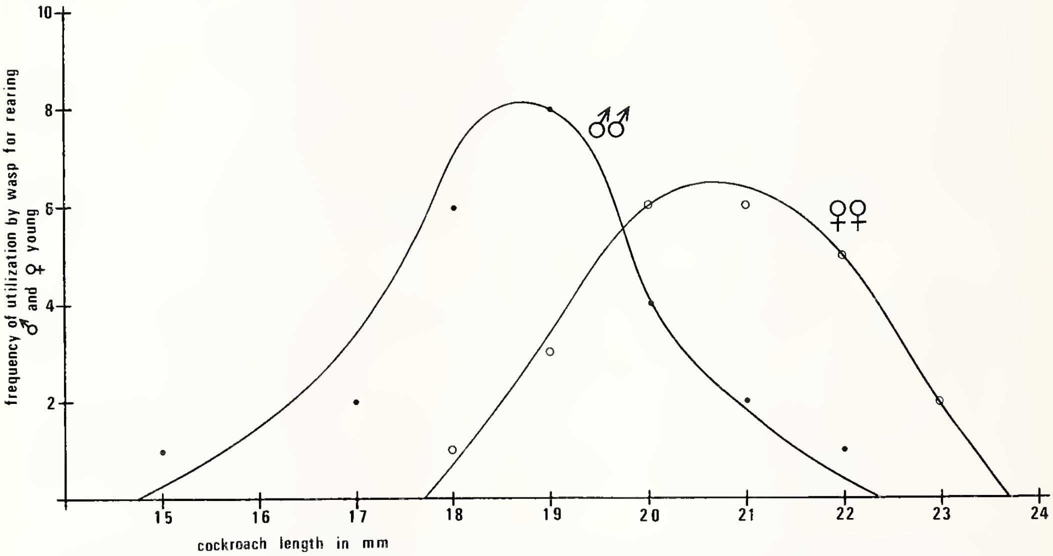


Fig. 15. Graphs to show differences in frequency of utilization (vertical axis) of different length categories (grouped to nearest mm) of *Bantua dispar* (horizontal axis) by *Ampulex bantuae* for rearing males and females.

a bearing upon whether an egg laid upon a cockroach will be male or female producing, that is unfertilized (haploid) or fertilized (diploid).

This situation is reminiscent of that recorded by Brunson (1938) for *Tiphia popilliavora* Rohwer developing upon the larvae of the Japanese beetle.

Three of the *A. bantuae* females reared in captivity were provided with trap-nests, nesting materials and cockroaches but were not allowed access to male wasps. These females gave rise to nine progeny all of which, having developed from unfertilized eggs, were males. The cockroaches utilized ranged from 16–23 mm in length. The size of the males produced was not in proportion to cockroach lengths nor did the length range of 8,3–11,3 mm exceed the normal range for males. That is, outsize males were not produced on prey above the size range normally used for rearing males.

THE EFFECT OF THE STING UPON THE PREY

The paralysing effect of the sting of *A. bantuae* on its *B. dispar* prey appears to pass off rapidly and possibly completely. The recovery of the cockroaches from the initial knock-down, evident immediately after stinging, to the state in which they can be led to the nesting cavity has been described. Frequently a stung cockroach, positioned by a wasp at the inner end of a trap-nest, backs along the length of the cell in which it is sealed until its further progress is stopped by the detritus cell closure. Furthermore a stung cockroach bearing an *A. bantuae* egg or young larva readily escapes from the cell when the trap-nest lid is lifted. This causes difficulty when measuring the eggs and recording their position as cockroaches when removed from cells and laid upon their backs immediately right themselves and walk away. It appears therefore that the detritus cell closure is as important in keeping the cockroach in as it is in keeping other insects out.

Two adult female cockroaches laid oothecae some days after being stung. One, found sealed in a trap-nest at Hilton on 25.xi.1973 and bearing an egg, laid a 12 mm long ootheca containing twenty eggs on 9.xii.1973. The wasp larva which hatched on 27.xi.1973 died on 9.xii.1973 after developing very slowly. The cockroach died on 19.xii.1973. The eggs in the ootheca developed but the nymphs failed to hatch. The other, a captive, was stung on 11.iv.1974 but not oviposited upon. It was observed feeding on 13.iv.1974 and it subsequently laid an ootheca from which nymphs hatched on 18.iv.1974.

Moulting by a stung cockroach was observed. The cockroach, a female bearing an egg, was found sealed in a trap-nest at Hilton on 29.i.1975. The egg failed to develop and consequently the cockroach remained alive. It moulted on 10.iii.1975 and although confined within a gelatine capsule without any food was still active on 1.iv.1975.

DISCUSSION

Some details of the hunting and nesting behaviour of nine of the 118 species of *Ampulex* recognized by Bohart and Menke (1976) have been published to date. The species, arranged in alphabetical order, and the publications relevant to each are:

A. assimilis Kohl (Hingston, 1925), *A. canaliculata* Say (Williams, 1929; Krombein, 1967), *A. compressa* (Fabricius) (Réaumur, 1742; Lucas, 1879; Bingham, 1897; Maxwell-Lefroy, 1909; Bordage, 1912; Williams, 1942), *A. compressiventris* Guérin-Méneville (Sharp, 1901, as *A. sibirica), A. dissector* (Thunberg) (Sonan, 1927; Kamo, 1957; Kohriba, 1957; Yoshikawa and Iida, 1956; Yoshikawa, 1957; in all cases as *A. amoena* Stal), *A. fasciata* Jurine (Picard, 1911 and 1919), *A. nigrocaerulea* Saussure (Callan, 1976), *A. ruficornis* (Cameron) (Sharp, 1901) and *A. sonnerati* Kohl (Sonnerat, 1776). The earlier published accounts of *Ampulex* biology were reviewed by Williams (1929 amd 1942). Other secondary sources are Clausen (1940), Iwata (1976) and to a minor extent Guthrie and Tindall (1968).

The nesting ethology recorded during the course of the present study does not differ to any significant extent from that published for the above listed species. Indeed, on the basis of present knowledge, it appears that the ethology of *Ampulex* is characterized by marked interspecific uniformity. It is, moreover, primitive in several respects. Notably, there is no preparation of a nest prior to hunting, nor indeed is a nest in the true sense constructed at any time. Nesting is within a pre-existing cavity which is neither cleaned out, expanded nor in any way modified to receive the prey. Thus in the present study it was found that foreign objects within trap-nests were not removed prior to prey introduction nor was a preliminary plug ever constructed even when the inner end of the trap-nest was already occupied by the cells of leafcutting *Megachile* species. Cavity modification is limited solely to its closure by the construction of a detritus plug following the positioning of the prey and oviposition upon it.

Consideration of the sequence of behavioural elements in the nesting of *Ampulex*, prey—niche—egg—closure, makes it clear that each sealed cell must be regarded as constituting a complete nest. Multicellular nests therefore do not exist. Where several cells occur in a single cavity as has sometimes been recorded (e.g. in Krombein, 1967 and in the present study) each cell represents a separate and possibly unrelated instance of nesting, not necessarily even by one and the same female.

It would appear that *Ampulex* species are essentially arboreal wasps, hunting their prey on shrubs and trees and nesting within niches present on these plants. The nesting ethology of *A. bantuae* described in the present paper is paralleled to a remarkable extent by that of *A. assimilis*, studied in Iraq by Hingston (1925). This wasp was found to hunt the wingless females of the cockroach *Shelfordella tartara* Saussure on the trunks of date palms and to nest within old beetle borings in the trunks. Similarly another species, *A. compressa*, was recorded by Maxwell-Lefroy (1909) as hunting *Periplaneta* species on the trunks of old Peepul (*Ficus religiosa*) trees in India. One hole and chink after another was searched for cockroaches and it may be assumed that these cavities were used by the wasp for nesting. Williams (1942) recorded the same species frequenting the trunk of a coconut palm in New Caledonia. The fact that Krombein (1967) in North America found *A. canaliculata* utilizing trap-nests suspended 1 to 2 metres above ground from dead limbs of loblolly pines is indicative that this wasp and the cockroaches hunted by it, *Parcoblatta* species, are also arboreal. The same conclusion may be applied to *A. fasciata* found in France to prey upon *Ectobia livida* Fabricius and to nest inside bramble stems hollowed out, it was believed, by solitary bees (Picard, 1911) and in insect borings in fig trees (Picard, 1919).

However, several species preying upon synanthropic cockroaches appear to have followed their prey into human habitations. Thus *A. compressa*, above recorded as arboreal, is more commonly recorded as hunting its prey, *Periplaneta* species, in houses. Records exist from Mauritius (Réaumur, 1742), Burma (Bingham, 1897) and Réunion (Bordage, 1912). Similarly *A. compressiventris* in West Africa (Sharp, 1901) and *A. sonnerati* (Sonnerat, 1776) in the Philippines were recorded hunting inside buildings. In all cases nesting took place in crevices situated within the buildings. It is probable that *A. dissector* of Formosa and Japan, which like *A. compressa* preys on *Periplaneta* species, similarly hunts and nests in buildings.

Bohart and Menke (1976) have remarked that, with the exception of *A. sikkimensis* (Kriechbaumer), all species of *Ampulex* seen by them have modified tarsomeres. Thus the penultimate or fourth tarsomere has a ventral hair mat but lacks apical setae and the last tarsomere is inserted dorsally near the base of the fourth. This modification and configuration of the tarsomeres, exhibited also by *A. bantuae*, is very similar to that found in adult Coleoptera of the superfamilies Cucujoidea, Chrysomeloidea and Curculionoidea which normally live on the aerial parts of plants and is clearly an adaptation to an arboreal life.

As *Ampulex* provisions each nest with but a single prey, it follows that the latter is of necessity both larger and heavier than the wasp itself. A consequence of this disparity in size

and weight is that the wasp is unable to pick up the prey and carry it to the nesting cavity. The dragging of a deeply paralysed, inert prey to the nest as practised by the majority of Pompilidae, which, like *Ampulex*, provision each cell with a single large prey, is practicable if the way to the nest is over the ground. However, in an arboreal situation such as that in which *Ampulex* hunts and nests this method of prey transport is not possible for the prey or the wasp and the prey together could easily fall to the ground. *Ampulex* has overcome the problem in a unique manner—by enlisting the co-operation of the prey itself. The effect of the *Ampulex* venom upon the prey is not to paralyse but rather to tranquilize it so that at the time of its transport to the nesting cavity.it is incapable of any initiative or independent action such as would be required for escape. However, when grasped by the wasp by an antenna and pulled, the prey is capable not only of walking but, in walking, of clinging to the substrate and therefore of preventing itself from falling to the ground. In *Ampulex*, adaptations for an arboreal life are therefore not only morphological (the modified tarsomeres) but also biochemical (the nature of the venom) and behavioural (the nature of prey transport).

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p. 45 - line 20 - delete after (Pfeffer, 1889) "and later figure (Pfeffer, 1889)"

p. 50 - 2nd paragraph, line 4 : Pietschmann 1973 = 1913

- 5th paragraph, line 4 : 1,1 - 3 = 1 - 1,3

p. 57 - 1st paragraph, line 5 : 5 + 6 = 5 - 6

line 6 : ph - 1 + 2 = ph + 1 $\pm$ 2

p. 58 - table 6A in title : spelling Hypural

table 6B - allign N vertically.

p. 68 - Acknowledgements, line 5 : spelling Audenaerde

p. 69 - reference Matthes 1967 : E.A.F.F.R.O.

A systematic revision of species of the catfish genus *Amphilius* (Siluroidei, Amphiliidae) from east and southern Africa

by

P. H. SKELTON

(Albany Museum, Grahamstown)

ABSTRACT

The taxonomy of *Amphilius* species from east and southern Africa is reviewed. A gross misidentification of *Amphilius platychir* (Günther) is exposed and corrected. *A. grammatophorus* is placed in synonymy with *A. platychir*. The name *A. uranoscopus* is recalled for the most common and widespread east and southern African *Amphilius* species. Distinguishing characters of *A. natalensis* Boulenger are identified and the species is shown to include the population of *A. lampei* from Zimbabwe. A new *Amphilius* species is recognized and described from the Buzi River in Mocambique.

INTRODUCTION

In the last revision of *Amphilius* from southern Africa Bell-Cross & Jubb (1973) recognized three species. *Amphilius platychir* (Günther, 1864), the most common species, occurs from the Pongola River in Natal northwards to central and east Africa (Fig. 1). *Amphilius natalensis* Boulenger (1917) is more restricted. It is distributed from the Umkomaas River northwards to the Incomati system and is present in the Marozi River a tributary of the Zambezi River arising in the Inyanga highlands of Zimbabwe (Bell-Cross & Jubb, 1973). *Amphilius lampei* Pietschmann (1913) was discovered isolated above a high waterfall in a short stretch of the Nyazengu River, a tributary of the Pungwe system in the eastern highlands of Zimbabwe. Prior to this *A. lampei* was only known from the type locality, a mountain stream near Harar in Ethiopia (Fig. 3).

Surveys of the eastwards flowing rivers of the Transvaal by the provincial nature conservation authorities in the late 1960's first revealed that *A. natalensis* was present in the Incomati and Pongola systems (Gaigher & Pott, 1972). The species was recently discovered in the Blyde River, a Limpopo tributary (Kleynhans, 1979), and the Ruo River, draining from Mount Mhlange in Malaŵi to the Lower Shire–Zambezi system (BMNH 1978. 12.13: 13–14). Both *A. natalensis* and *A. platychir* show a great deal of morphological variation and are easily confused in the field and, as the present investigation shows, by museum specialists as well. There is thus a need to investigate and expose more clearly the distinguishing characteristics of each species. Re-identification of museum samples indicates an extension of range of *A. natalensis*.

The most outstanding feature of *A. lampei* is the long low adipose fin confluent with the anterior ridge-like extension of the caudal fin (Bell-Cross & Jubb, 1973). The adipose fin varies considerably between *A. natalensis* populations and includes an *A. lampei* form in several of them. In view of this and other more definitive characters the identity of the Nyazengu *A. lam-*

pei is re-assessed in this paper. An unexpected outcome of the study is the discovery of an undescribed species from the lower reaches of the Buzi River in Mozambique.

These studies form part of a wider investigation of the phylogeny and biogeography of the family Amphiliidae. This broader study has involved, *inter alia*, the examination of the majority of available type specimens of amphiliid species. Several taxonomic discrepancies have been exposed in the process, the most serious involving the identity of *A. platychir*, the first amphiliid to be described. The paper considers and corrects the taxonomic record for the east and southern African *Amphilius* species.

Materials

The type specimens of nominal species connected with the taxonomy of southern African *Amphilius* (Table 1) were measured, examined and x-rayed. Additional material from the collections of the Albany Museum (AMSA) and National Museum of Zimbabwe [formerly Queen Victoria Museum (ZNM)] were also examined, measured and x-rayed (Appendix 1).

Table 1

Amphilius type specimens examined

Species	No. specimens examined	Reg. No.
Amphilius platychir	4	BM(NH) Not Registered
	1	MNHN 1898–121
Amphilius uranoscopus	2	NMH 11944
Amphilius leroyi	1	MNHN 1897–3
Amphilius grandis	3 (2)	BM(NH) 1904.12.23: 50–52
Amphilius hargeri	1	BM(NH) 1907.10.14: 8
Amphilius krefftii	2	BM(NH) 1909.10.19: 26–27
Amphilius oxyrhinus	1	BM(NH) 1912.3.22: 120
Amphilius grammatophorus	5	MNHN 1913–231–235
Amphilius brevidorsalis	1	MNHN 1919–488
Amphilius platychir cubangoensis	4	MNHN 1936–101–103. MRAC 138769
Amphilius natalensis	1	BM(NH) 1917.7.21: 1. Second specimen not traced
Amphilius lampei	1	NMW 48094 (Paratype; Holotype not traced)
Amphilius kivuensis	3	MNHN 1932–38/1933–9–11

Abbreviations:
- BM(NH) — British Museum (Natural History).
- MNHN — Museum National d'Historic Naturelle, Paris.
- NMH — Naturhistorisches Museum, Hamburg.
- NMW — Naturhistorisches Museum, Wien (Vienna).
- MRAC — Museum Royale d'Afrique Centrale, Tervuren.

Methods

Linear measurements follow the methods of Skelton (1981). The additional measurement of 'Head to Dorsal fin' is taken from the posterior margin of the head to the anterior base of the dorsal fin. Vertebral counts were taken from radiographs according to Skelton (1976) except that all counts exclude 1–4 Weberian vertebrae. The first caudal vertebra was taken as that with a distinct haemal spine. Specimens were cleared and stained for bone and cartilage study according to the methods of Taylor (1967) and Taylor & Van Dyck (1979).

TAXONOMY AND IDENTITY OF *AMPHILIUS PLATYCHIR*

Günther (1864) described five smallish catfish specimens from Sierra Leone under the name of *Pimelodus platychir* (Fig. 1A). The following year Günther (1865) restricted *Pimelodus* to South America and renamed his African species *Amphilius platychir. Anoplopterus uranoscopus*, a somewhat similar species, was described much later by Pfeffer (1889) from the Wami and Pangani River in Tanzania (Fig. 1B). Pfeffer (1896) overlooked Günther's (1865) generic change and brought *A. platychir* into the genus *Anoplopterus*. Vaillant (1897) described a third species, *Chimarrhoglanis leroyi*, from Tanzania (Fig. 1C). Boulenger (1898) referred specimens from Nyasaland (now Malaŵi) to the species *A. platychir* and questioned Günther's (1864) statement that the types of the species were collected in Sierra Leone. Boulenger (1898) also synonymized Vaillant's *C. leroyi* with *A. platychir* and recognised Pfeffer's *A. uranoscopus*. Poche (1902b) drew attention to the priority of *Amphilius* as the correct name for the genus. Poche (1902a) and Günther (1902) refuted Boulenger's (1898) suggestion that the types of *A. platychir* were not from Sierra Leone.

Boulenger (1911) ignored these refutations in his influential catalogue and gave the distribution of *A. platychir* as "East Africa, westwards to Lake Tanganyika and Nyasa". Boulenger described several other *Amphilius* species from east Africa: *A. grandis* (1905) (Fig. 1D), *A. hargeri* (1907) (Fig. 1E), *A. kreffti* (1911) (Fig. 1F), and *A. oxyrhinus* (1912) (Fig. 1G). These were all very similar, differing only in minor proportions (Table 2) and have usually been dubiously recognized by authors (e.g. Harry, 1953; Bailey, 1969). Apart from some discussion of *A. hargeri* (see below) they are here considered to be synonyms of a single common widespread species from east and southern Africa.

Two species and one sub-species described by Pellegrin are also implicated in the taxonomy of *A. platychir*. Pellegrin (1913, 1919) described *A. grammatophorus* from the Konkoure River in French Guinea (Fig. 1H) and *A. brevidorsalis* from the Revue River (Buzi River system) in Mocambique (Fig. 1I). The subspecies *Amphilius platychir cubangoensis* was described from the 'Cubango' or Okavango River in Angola by Pellegrin (1936) (Fig. 1J).

Crass (1960) and Jubb (1961) followed Van der Horst (1931) who referred specimens from Transvaal rivers to *A. grandis*, but Jackson (1961), Crass (1964), Jubb (1967) and Bell-Cross & Jubb (1973), all probably under the influence of Boulenger's (1911) catalogue, considered the species to be *A. platychir* (see Bell-Cross & Jubb, 1973). Following Jubb (1967) and Bell-Cross & Jubb (1973) the common species of southern Africa is therefore currently accepted as being *A. platychir*. Elsewhere the species was also usually referred to as *A. platychir* (e.g. Poll, 1953, 1967, 1976; David & Poll, 1937; Ricardo, 1939; de Kimpe, 1964; Marlier, 1954; Matthes, 1967).

Apart from the type specimens and the collection referred to by Poche (1902a) *A. platychir* has not been reported from West Africa. Only a single specimen in the British Museum collection (BMNH 1968. 9.17: 3) from Sierra Leone has been subsequently referred to *A. platychir*. The 'common' *Amphilius* from this region in West Africa is identified and generally referred to *A. grammatophorus* (e.g. Norman, 1932; Daget, 1962; Daget & Iltis, 1965).

In view of Günther's (1902) public assertion that the type locality of *A. platychir* is Sierra

Fig. 1. Type localities of certain *Amphilius* species and range of *A. uranoscopus* (see text). Type localities

(A) *A. platychir* (Günther);	[F] *A. krefftii* Boulenger;
[B] *A. uranoscopus* (Pfeffer);	[G] *A. oxyrhinus* Boulenger;
[C] *A. leroyi* (Vaillant);	(H) *A. grammatophorus* Pellegrin;
[D] A. grandis Boulenger;	[I] *A. brevidorsalis* Pellegrin;
[E] *A. hargeri* Boulenger;	[J] *A. platychir cubangoensis* Pellegrin.

Stippled area represents range of species herein recognized as *A. uranoscopus* (Pfeffer).

Leone the identity of the species in east and southern Africa is clearly in dispute. Close examination of the type specimens revealed an unequivocal character of the caudal fin which places beyond doubt the true identity of *A. platychir* as a west African species. The caudal fin of the type specimens of *A. platychir* has only 6 + 7 principal rays and features a prominent crenellated fold along the base on either side (Table 2; Fig. 2). All east and southern African *Amphilius* sp. have 8 + 9 principal rays and do not have a flap or fold along the base. Although this flap of skin has been reported for certain *Amphilius* sp. (e.g. Trewavas, 1936), it has generally been overlooked or neglected as a character in *Amphilius* descriptions. The flap is characteristic of most west African *Amphilius* sp., certainly of all species known from the Sierra Leone region, a fact which vindicates Günther's opinion and disproves Boulenger (1898) and subsequent authors who record *A. platychir* from east and southern Africa.

There is consequently a problem as to the correct name for the several nominal species from east and southern Africa (Fig. 1). The usual choice of authors has been *A. grandis* but, as shown above, at least two east African species were described prior to *A. grandis*, namely *A. uranoscopus* Pfeffer (1889) and *A. leroyi* Vaillant (1897). *A. uranoscopus* has always been held distinct by authors (e.g. Boulenger, 1911; Harry, 1953; Bailey, 1969) mainly on account of its, as described, relatively small head ($\frac{\text{SL}}{\text{HL}}$ = 5,3 v. 4,3 in *A. platychir*). *A. leroyi* on the other hand was made a junior synonym of "*A. platychir*" from an early date by Boulenger (1898) and subsequently widely accepted as such (e.g. Poche, 1902; Boulenger, 1911; Harry, 1953). When judged from the original description (Pfeffer, 1889) and later figure (Pfeffer, 1889) and later figure (Pfeffer, 1896; Boulenger, 1911) the type specimen of *A. uranoscopus* is apparently distinct on the basis of head size from that of *A. platychir* and *A. leroyi*. However, there is an important discrepancy between the type specimen and Pfeffer's description. Pfeffer (1896) stated that the headlength was contained 5,3 times in the body length *without* the caudal fin. The present author's measurements of the type specimen (Table 2) give the head length as contained 4,2 times in the standard length. Several other measurements taken also disagree with Pfeffer's (1889; 1896) descriptions, e.g. the nares are approximately once the orbit diameter apart (not twice), the posterior nare is nearer the end of the snout than the anterior border of the eye. The examination of the type of *A. uranoscopus* (Table 2) indicates clearly that it is the same species as *A. leroyi*, *A. grandis* and other nominal east African forms. By the law of priority therefore the correct name for this species is *Amphilius uranoscopus* (Pfeffer, 1889).

In the original description of *Amphilius grammatophorus*, Pellegrin (1913) drew attention to the close affinities this species had with Günther's *A. platychir*. Pellegrin considered the two species to differ in the position of the dorsal fin (the hind margin anterior to the origin of the pelvics in *A. platychir*, the hind margin over the origin of the pelvics in *A. grammatophorus*), the slightly shorter maxillary barbel in *A. platychir* and the relatively shorter caudal peduncle in *A. platychir* (C.P. "a little longer than deep in *A. platychir*" and 1,75–2 times longer than deep in *A. grammatophorus*).

A morphometric and meristic comparison of the type specimens of these species is given in Table 2. This comparison is offset to a certain degree by the difference in overall size of the two sets of types (SL range of *A. platychir* 35,5–44,1 mm; 56–91,5 mm in *A. grammatophorus*). The differences between the types are not marked and in most eases are not diagnostic. Possibly the clearest differences are the predorsal distance, head width and preanal vertebrae. The longer predorsal length of *A. platychir* does not correlate with any clear vertebral difference at least in the predorsal part of the vertebral column. In general body and fin ray characteristics including the caudal fin and the associated fleshy flap described above, the types of the two species are similar. The types of *A. grammatophorus* do have a greater number of gill rakers than those of *A. platychir*. The age and condition of the types of *A. platychir* could well be

TABLE 2

Comparison of morphometric and meristic characters of the types of *Amphilius platychir* (Günther) and *Amphilius grammatophorus* Pellegrin.

CHARACTER	*A. platychir* $\bar{M}$	N=5 Range	*A. grammatophorus* $\bar{M}$	N=5 Range
Measurements				
Standard length (mm)		35,5–44,1		56,0–91,5
As % Standard length				
Predorsal length	42,0	41,2–43,7	37,4	36,6–38,5
Head length	24,7	23,2–25,9	22,2	20,4–24,3
Head depth	10,4	9,3–12,1	10,0	9,2–11,1
Head width	21,5	20,7–22,5	19,6	18,7–20,6
Body depth	11,6	10,7–13,5	14,3	12,5–16,6
Body width	15,3	13,6–16,0	15,5	14,1–16,7
Caudal peduncle length	16,6	15,1–17,7	18,0	16,8–19,5
Caudal peduncle depth	10,2	9,3–10,6	9,1	8,4– 9,6
Dorsal fin length	20,8	18,1–21,8	20,0	19,1–21,4
Anal fin length	18,6	17,6–19,3	17,7	16,4–18,2
Pectoral fin length	22,2	21,3–22,8	19,3	18,3–20,3
Pelvic fin length	20,2	19,0–21,1	18,0	17,1–18,6
As % Head length				
Snout	51,3	49,5–53,2	55,4	51,8–58,5
Orbit	12,1	10,3–14,9	10,9	9,4–12,3
Interorbit	32,2	29,4–34,8	33,7	31,4–35,0
Postorbit	42,3	41,3–43,6	39,9	38,5–41,4
Maxillary barbel	80,1	70,9–90,4	86,3	76,6–98,5
Mandibular barbel (inner)	34,3	30,9–39,4	47,4	40,1–53,8
Mandibular barbel (outer)	54,9	50,6–57,8	68,8	61,3–76,4
Fin Ray Counts				
Dorsal fin	i,5(1); i,6(4)		i,6(5)	
Anal fin	ii,5(2); ii,6(3)		ii,6(4); ii,7(1)	
Pectoral fin	i,8(2); i,9(3)		i,8(5)	
Pelvic fin	1,5(5)		i,5(5)	
Caudal fin	6 + 7(5)		6 + 6(1), 6 + 7(2)	
Gill rakers (Ant. Arch)	2 + 4(1); 2 + 6(1); 1 + 6(1); 2 + 7(1)		2 + 8(4); 4 + 7(1)	
*Vertebral Counts**				
Total vertebrae	33(2), 35(3)		34(5)	
Precaudal vertebrae	14(1), 15(3), 16(1)		13(2), 14(3)	
Caudal vertebrae	18(1), 19(2), 20(2)		20(3), 21(2)	
Predorsal vertebrae	3(3), 4(2)		4(5)	
Preanal vertebrae	21(4), 22(1)		18(1), 19(4)	
Hypural pattern	Ph+1+2−3+4−5+6(3)		Ph+1+2−3+4−5+6(5)	

*Vertebral counts exclude 1–4 Weberian vertebrae.

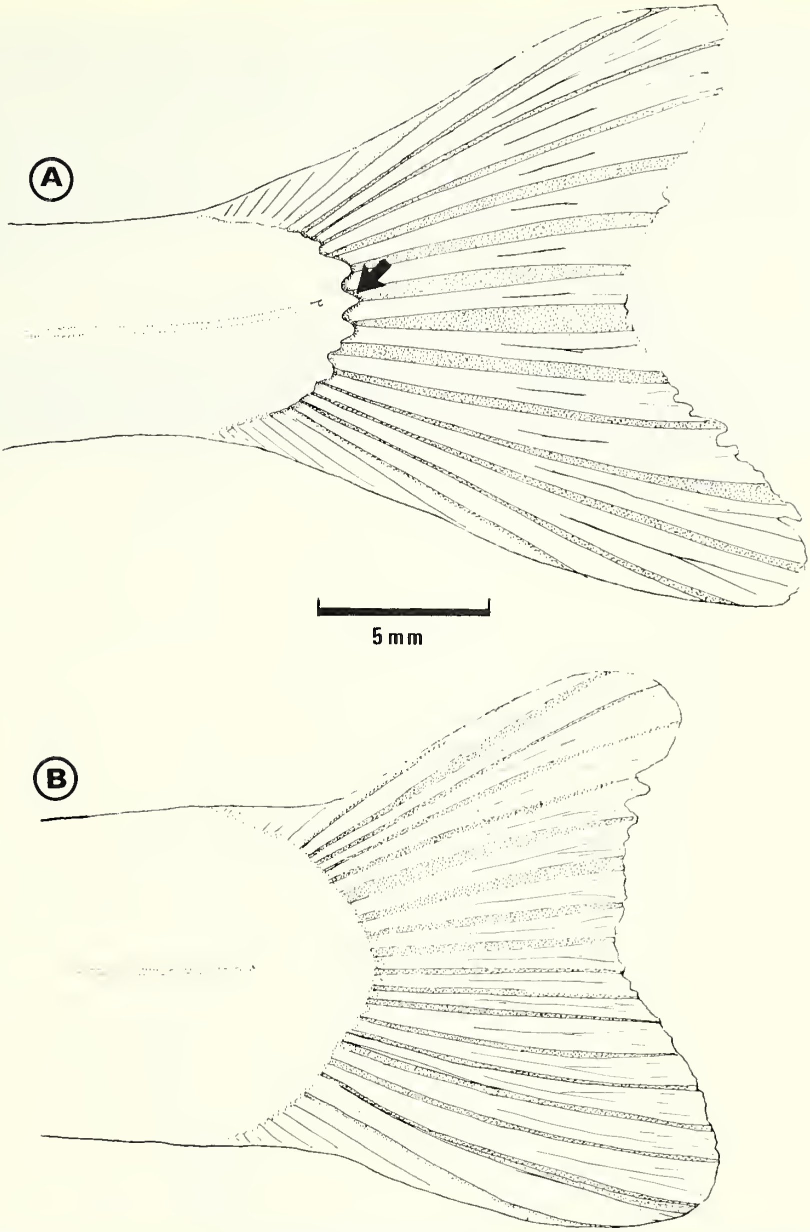


Fig. 2. Caudal fin of A) *Amphilius platychir* (AMSA/P 9559) from Konkoulo à Pita, Guinea collected by C. Leveque 28.04.1980R, and B) *Amphilius uranoscopus* (AMSA/P 6207) from Olifants River, Limpopo River system. Arrow indicates crenellated flap characteristic of west African *Amphilius* species including the types of *A. platychir*.

a factor influencing the measurements and it is not easy to make a clear taxonomic decision. This is aggravated by the paucity of available specimens of *A. platychir* from west Africa. In spite of the above mentioned differences between the types there remains little reasonable doubt that *A. grammatophorus* is a junior synonym of *A. platychir*.

THE STATUS OF *AMPHILIUS LAMPEI* IN SOUTHERN AFRICA

The recording of *Amphilius lampei* from the Nyazengu River, a tributary of the Pungwe system near Inyanga in eastern Zimbabwe, by Bell-Cross & Jubb (1973) was certainly one of the most surprising and difficult-to-explain ichthyological discoveries from the sub-continent. As pointed out by Bell-Cross & Jubb (1973) the type locality near Harar in Ethiopia is likely to be a tributary of the Webi Shebeli system (Fig. 3).

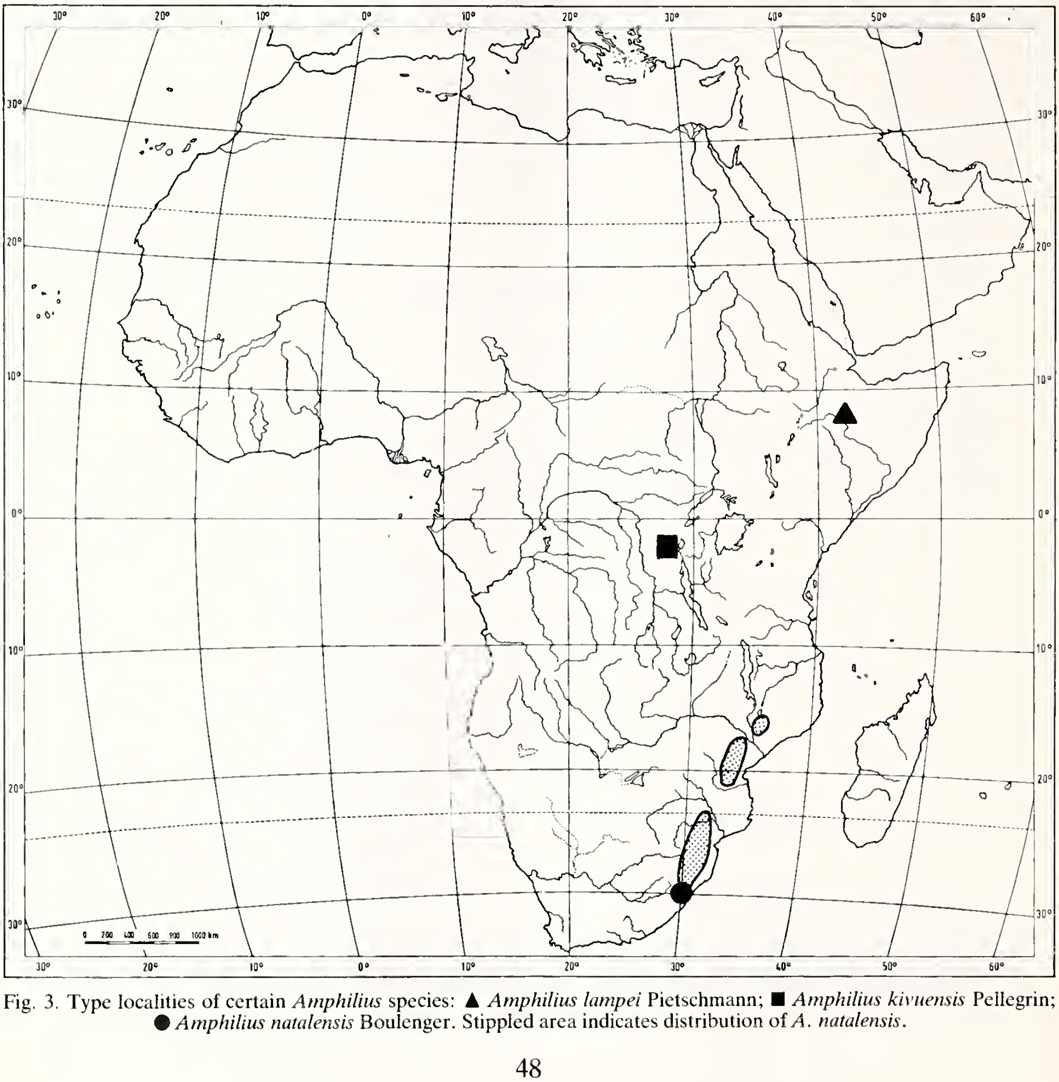


Fig. 3. Type localities of certain *Amphilius* species: ▲ *Amphilius lampei* Pietschmann; ■ *Amphilius kivuensis* Pellegrin; ● *Amphilius natalensis* Boulenger. Stippled area indicates distribution of *A. natalensis*.

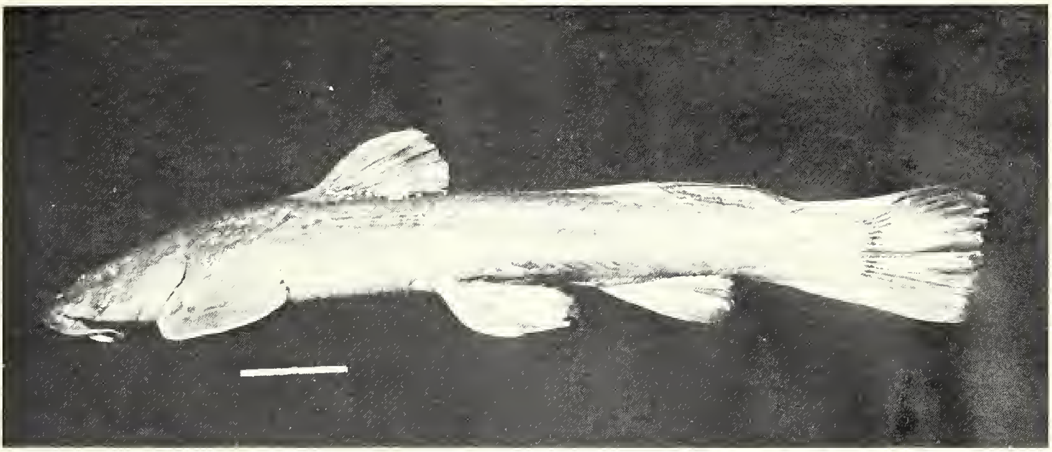


Fig. 4. Paratype of *Amphilius lampei* Pietschmann (NMW 48094; SL 76 mm). (Holotype and only other known specimen of this species from type locality is missing, presumably lost during World War II). Scale bar = 1 cm.

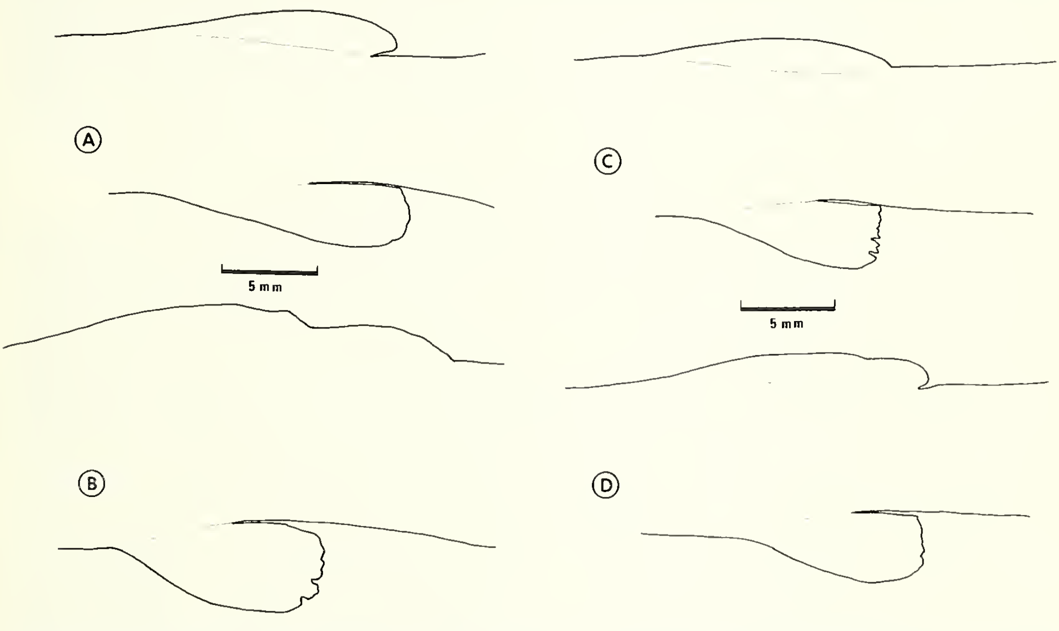


Fig. 5. Form of adipose fin in *Amphilius*: A) *A. natalensis* from the type locality, Umgeni River at Krantzkloof (AMSA/P 9557); B) *A. natalensis* from Nyazengu River, Pungwe system, Zimbabwe (*A. lampei sensu* Bell-Cross and Jubb, 1973) (Q.V.M. 2743); C) *A. natalensis* from Pungwe River (AMSA/P 5814); D) *A. uranoscopus* from Pungwe River (AMSA/P 5814).

A key feature of *A. lampei* is the long low confluent adipose fin (Fig. 4). In this the Nyazengu population was shown to differ markedly from the short adipose with a distinct posterior 'nick' or notch of *A. uranoscopus* (= *"platychir"*) found elsewhere in the Pungwe system (Fig. 5D). At the time Bell-Cross & Jubb (1973) did not realize that both *A. uranoscopus* and *A. natalensis* occur in the Pungwe River below the Nyazengu waterfall (see also Bell-Cross, 1976; Bowmaker *et al.*, 1978). However, examination of collections in the Albany Museum (Appendix 1) shows that both species are present in the Pungwe. The adipose fin of *A. natalensis* from the Pungwe (Fig. 5C) is low and not nicked like that of *A. uranoscopus* (Fig. 5D).

This discovery of *A. natalensis* in the Pungwe and the fact that there was no great difference between the adipose fin of *A. natalensis* and that of *A. lampei* necessitated a comparison of the two species. However, before doing this the taxonomic weight which has previously been given to the form of the adipose fin in amphiliids (e.g. discussions by Pietschmann, 1973; Barnard, 1942; Harry, 1953; Bell-Cross & Jubb, 1973) requires that further detail be provided on the form of the fin in *A. natalensis*.

In Natal populations the adipose fin in adult *A. natalensis* is short and has a posterior 'nick' as shown in Fig. 5A, and in published photographs and figures (Jubb, 1967 Fig. 168; Bell-Cross & Jubb, 1973 Fig. 1; Fowler, 1934 Fig. 3). In the Pongola system and rivers to the north the adipose fin does not have a free posterior edge but is more or less confluent with the anterior extension of the fleshy caudal fin fold. In some populations e.g. those of the Blyde and Mtarazi rivers, the adipose fin is relatively long and extremely similar to the form it takes in the Nyazengu *"A. lampei"* (Fig. 5D) and the type specimen of *A. lampei* (Fig.4). Thus, this character cannot be used to distinguish Nyazengu *Amphilius* from *A. natalensis*. Further the Nyazengu *Amphilius* agrees in other diagnostic characters of *A. natalensis* (see below) indicating that only one species is involved. The real issue raised by these observations is therefore the identity of *A. natalensis (sensu lato)* and *A. lampei (sensu stricto)* in relation to each other. This issue is considered below after a clearer distinction between *A. uranoscopus* and *A. natalensis* has been made.

CHARACTER COMPARISON OF *AMPHILIUS URANOSCOPUS* AND *AMPHILIUS NATALENSIS*

Amphilius natalensis is usually reported to have a smaller head, to be more slender and to have the dorsal fin further back than does *A. uranoscopus* (Crass, 1964; Jubb, 1967; Bell-Cross & Jubb, 1973). Testing these characters (Figs 6, 7, 8, 9) indicates that the species differ as reported but that there is an overlap in range for all the measurements which reduces their absolute diagnostic value. Much of the confusion between the species evidently arises from the fact that workers tend to consider misleading proportions e.g. head width relative to head length (Fig. 10) or body width relative to body depth (Fig. 11). Contrary to the literature, the position of the dorsal fin as measured by the predorsal distance (Fig. 12) is the same for both species. What does differ, and is diagnostic, is the position of the dorsal fin relative to the hind margin of the head (Fig. 13).

Crass (1964) provided a key to distinguish the two species using a difference in head length relative to the distance between the head and the dorsal fin. In *A. uranoscopus* the length of head was given as 1,6–2 times the distance from gill opening to the anterior edge of the dorsal fin. In *A. natalensis* head length is 1,1–3 times this same distance. Crass' (1964) criterion, upheld here as probably the most clear external difference between the two species (Fig. 13), appears to have been overlooked by subsequent authors reporting southern African *Amphilius* species.

The significance of this character is stressed because of a clear skeletal difference underlying the external dimensions (Fig. 14). In *A. uranoscopus* the leading pterygiophore of the dorsal fin intercepts the vertebral column at the first, second or third post-Weberian vertebrae

TABLE 3

Morphometric ratios and meristic characters of type specimens of certain nominal East and Southern African *Amphilius* species

Character	*A. uranoscopus* (2)	*A. leroyi*	*A. grandis* (2)	*A. krefftii* (2)	*A. oxyrhinus*	*A. hargeri*	*A. brevidorsalis*
Measurements							
Standard length (mm)	117,5–124	118,0	137–162	47–87	167	48,5	43
As % Standard length							
Predorsal length	35,7; 36,5	34,7	34,6 ; 38	36,2 ; 33,8	38,3	41,2	37,7
Head length	23,8; 22,6	22,9	24,1 ; 25,5	21,9 ; 21,4	25,2	24,7	24,7
Head depth	10,0; 9,4	10,5	12,8 ; 13,0	13,2 ; 12,0	11,5	12,8	13,3
Head width	22,8; 20,8	22,2	23,4 ; 23,5	21,3 ; 20,8	22,2	22,7	21,4
Head length/Head to dorsal (Not % SL)	1,7; 1,5		1,84; 1,56	1,58; 1,55	1,75	1,3	1,56
Body depth	12,9; 12,1	15,8	15,7 ; 16,0	12,3 ; 12,6	12,9	14,4	15,6
Body width	18,7; 16,5	18,6	14,7 ; 17,2	15,1 ; 15,6	15,6	17,5	16,3
Caudal Peduncle length	18,5; 16,8	17,4	18,6 ; 19,5	18,3 ; 19,5	18,6	19,4	20,7
Caudal Peduncle depth	12,3; 11,9	11,9	9,9 ; 10,1	10,6 ; 11,5	9,3	11,1	10,7
Dorsal fin length	21,4; 18,6	17,5	15,0 ; 15,7	18,7 ; 17,9	15,6	21,4	20,0
Anal fin length	16,6; 17,7	16,1	12,0 ; 13,5	16,4 ; 16,3	16,2	18,6	16,7
Pectoral fin length	20,4; 20,3	19,9	16,8 ; 18,2	21,9 ; 19,7	18,6	22,1	21,7
Pelvic fin length	20,6; 18,9	18,3	14,5 ; 17,2	20,2 ; 19,0	15,6	20,4	19,8
As % Head length							
Head to dorsal 1.	14,0; 14,9		13,9 ; 15,4	13,8 ; 13,8	14,4	18,6	18,0
Snout	51,4; 54,3	54,1	51,3 ; 54,3	48,5 ; 50,5	52,9	50,8	47,2
Orbit	11,1; 9,6	11,5	11,5 ; 12,0	15,5 ; 11,3	9,5	10,8	11,3
Interorbit	25,7; 25,7	27,4	25,7 ; 29,0	30,1 ; 24,7	23,8	35,0	34,9
Postorbit	41,1; 42,9	40,7	41,0 ; 41,4	40,8 ; 41,4	41,9	46,7	42,5
Maxillary barbel	107,2; 82,1	96,3	51,0 ; 58,2	87,4 ; 91,4	59,5	116,7	78,3
Mandibular barbel (inner)	42,9; 35,7	50,0	28,6 ; 32,1	29,1 ; 37,6	32,1	49,2	30,2
Mandibular barbel (outer)	71,4; 71,4	68,5	41,0 ; 41,4	55,3 ; 59,1	45,2	83,0	49,1
As % Snout length							
Orbit to Post. nare	45,1; 49,3	54,8		48,0 ; 52,1	47,7		40,0
Post. nare to Ant. nare	15,3; 19,7	23,3		32,0 ; 26,6	19,4		24,0
Ant. nare to mid. snout	38,2; 32,9	41,1		38,0 ; 35,1	38,7		
Fin Ray Counts							
Dorsal fin	i,6; i,6	i,6	i,6; i,6	i,6; i,6	i,6	i,6	i,5
Anal fin	iii,6; iii,7	ii,6	iii,6; iii,6	ii,5; ii,7	iii,5	i,6	iii,5
Pectoral fin	1,10; 1,10(9)	1,10	1,10; 1,10	1,10; 1,10	1,10	1,10	1,10
Pelvic fin	1,5 ; 1,5	1,5	1,5 ; 1,5	1,5 ; 1,5	1,5	1,5	1,5
Caudal fin	8 + 9; 8 + 9	8 + 9	8 + 9; 8 + 9	8 + 9; 8 + 9	8 + 9	8 + 9	8 + 9
Gill rakers (ant. areh)	3 + 5; 3 + 6	4 + 7	3 + 7	1 + 6; 1 + 6	2 + 7	3 + 6	3 + 5
Vertebral Counts							
Total vertebrae	39; 38	36	38; 39	38	38	37	37
Precaudal vertebrae	16; 16	16	16; 17	16	17	16	16
Caudal vertebrae	23; 22	20	21; 23	22	21	21	21
Predorsal vertebrae	1; 0	2	2; 2	2; 2	2	3	0
Preanal vertebrae	22; 21	20	22; 22	21; 21	22	22	21

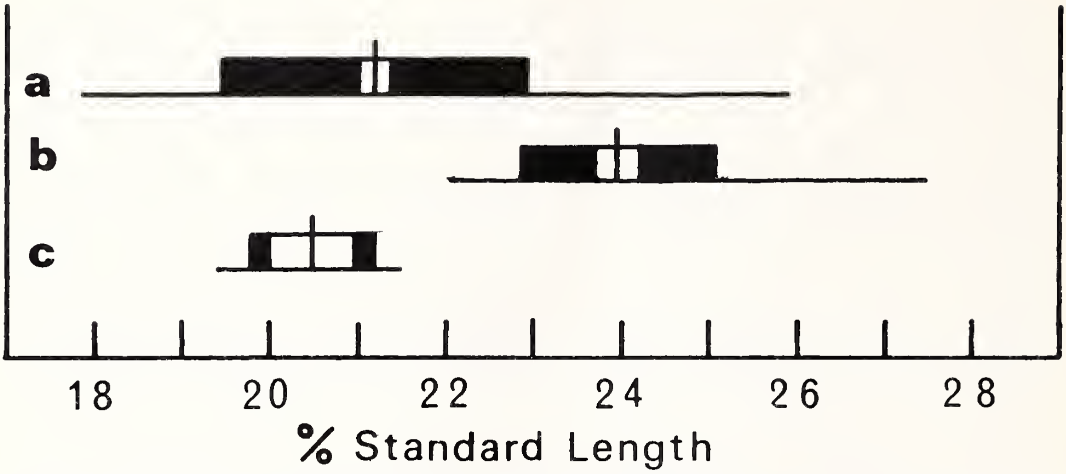


Fig. 6. Head length as % Standard length of (a.) *A. natalensis* (N=87) and (b.) *A. uranoscopus* (N=70) from different localities in southern Africa, and (c.) *A. natalensis* (= *A. lampei*) from Nyazengu River, Zimbabwe (N=10).

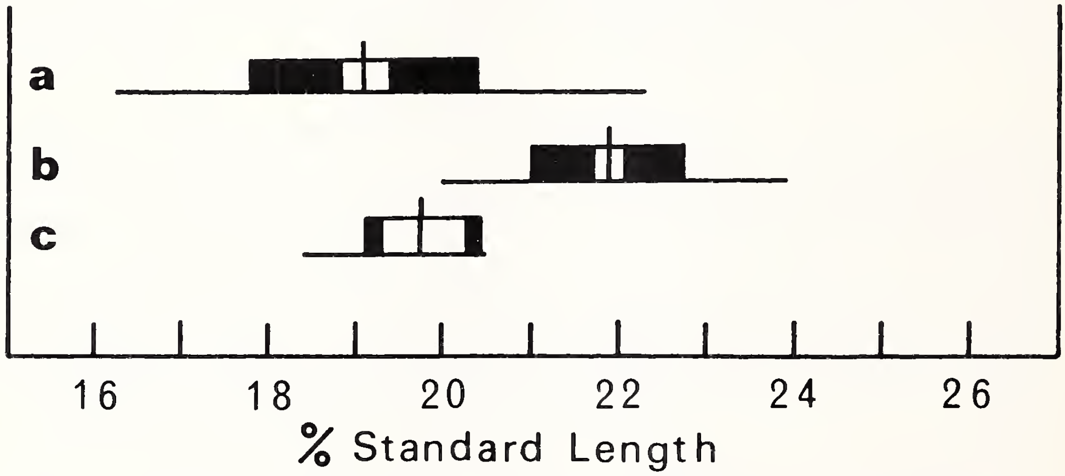


Fig. 7. Head width as % Standard length of (a.) *A. natalensis* (N=87); (b.) *A. uranoscopus* (N=70) from different localities in southern Africa, and (c.) *A. natalensis* (= *A. lampei*) from Nyazengu River, Zimbabwe (N=10).

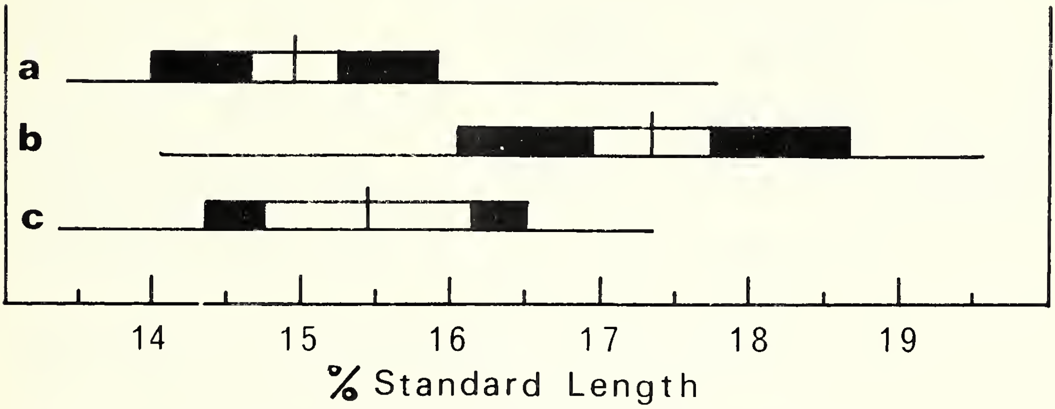


Fig. 8. Body width as % Standard length of (a.) *A. natalensis* (N=40); (b.) *A. uranoscopus* (N=44) from different localities in southern Africa and (c.) *A. natalensis* (= *A. lampei*) from Nyazengu River, Zimbabwe (N=10).

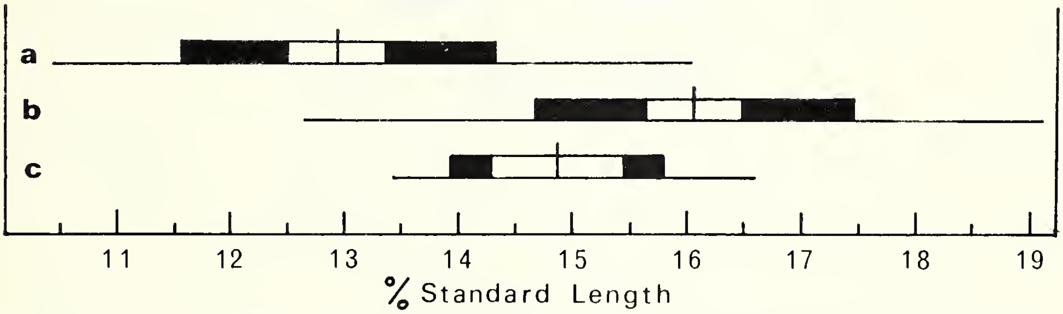


Fig. 9. Body depth as % Standard length of (a.) *A. natalensis* (N=40); (b.) *A. uranoscopus* (N=44) from different localities in southern Africa and (c.) *A. natalensis* (= *A. lampei*) from Nyazengu River, Zimbabwe (N=10).

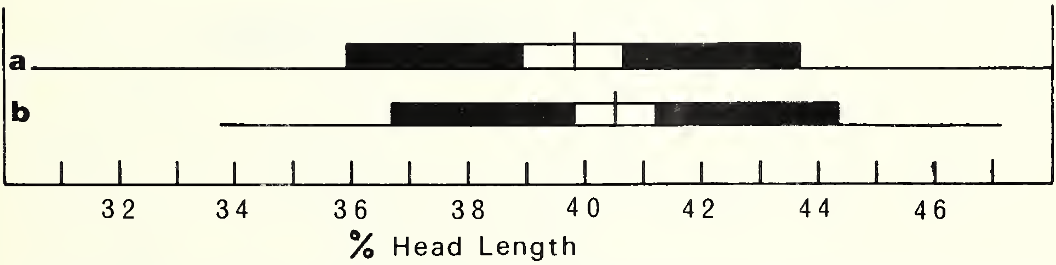


Fig. 10. Head width as % Head length of (a.) *A. natalensis* (N=87) and (b.) *A. uranoscopus* (N=70) from different localities in southern Africa.

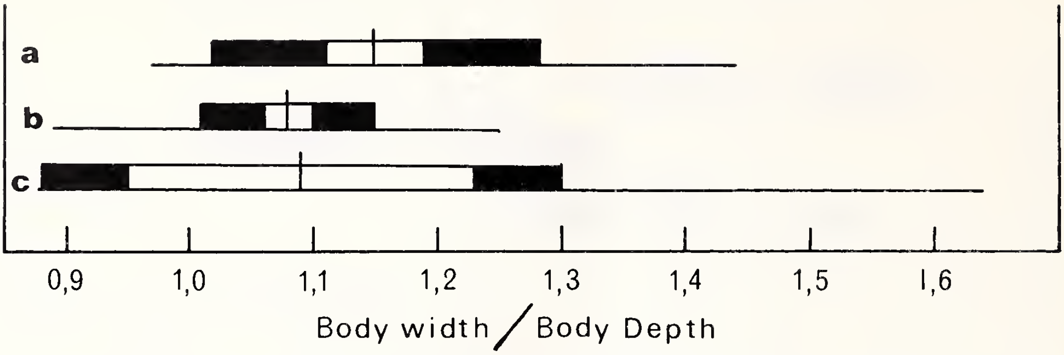


Fig. 11. Body width proportional to Body depth of (a.) *A. natalensis* (N=40); (b.) *A. uranoscopus* (N=44) from different localities in southern Africa and (c.) *A. natalensis* (N=10) from Nyazengu River, Zimbabwe.

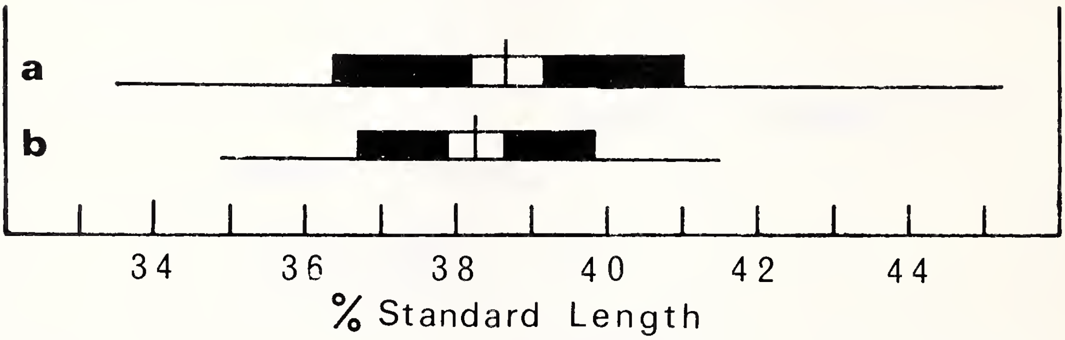


Fig. 12. Predorsal length as % Standard length for (a.) *A. natalensis* (N=87) and (b.) *A. uranoscopus* (N=70) from different localities in southern Africa.

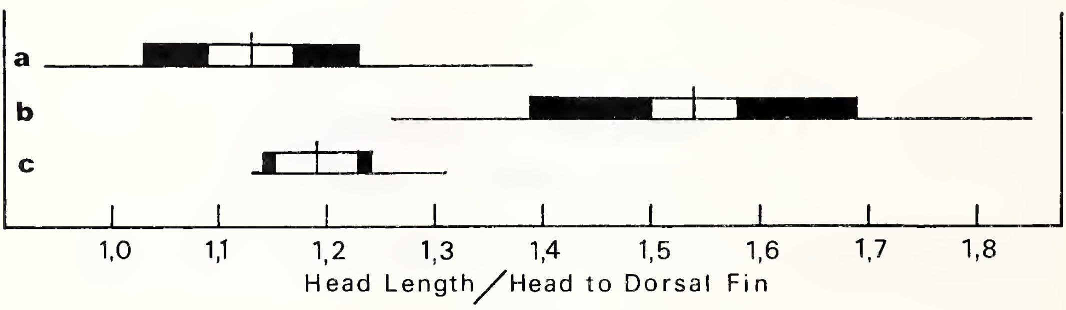


Fig. 13. Head length proportional to the distance between the head and dorsal fin of (a.) *A. natalensis* (N=40); (b.) *A. uranoscopus* (N=44) from different localities in southern Africa, and (c.) *A. natalensis* (= *A. lampei*) (N=10) from Nyazengu River, Zimbabwe.

(Fig. 14A, Table 5). By contrast there are four or five post-Weberian, pre-dorsal vertebrae in *A. natalensis* and, in support of the proposed synonymy, also in the upper Nyazengu *Amphilius* (Fig. 14B, Table 4).

There is an element of geographic variation in where the dorsal fin intercepts the vertebral column in *A. uranoscopus* (Table 4). In the type specimen as well as specimens from the Zambezi, Okavango, Pungwe and Save rivers, the first dorsal pterygiophore usually meets the first post-Weberian vertebra whereas in most other populations examined this pterygiophore meets the second or third post-Weberian vertebra. It is also noteworthy that in both the Save and the Limpopo systems different samples gave different results in this count. This suggests either divergent morphological trends within the systems or diverse origins of the stocks.

TABLE 4

Geographic variation in the distribution frequency of predorsal vertebrae* of *A. uranoscopus* and *A. natalensis* in southern Africa.

*excludes the 1–4 vertebrae of the Weberian complex.

		N	0	1	2	3	4	5	6
A. *Amphilius uranoscopus*									
Zambezi	Ruo	13			12	1			
	Gairezi	2	2						
	Okavango	25		24	1				
Pungwe		2		2					
Save	Sabi	10		10					
	Lundi	12			4	8			
Limpopo	Ndezele	3				3			
	Mooketzi	22				22			
	Steelpoort	9		9					
Pongola		11		1	7	3			
		109	2	46	24	37			
B. *Amphilius natalensis*									
Zambezi	Ruo	2				1	1		
	Gairezi	8				1	6	1	
Pungwe	Pungwe	13						13	
	Nyazengu	14					2	12	
Limpopo	Blyde	11						3	8
Incomati	Lunsklip	10						10	
	Incomati	6						3	3
Tugela	Ngogo	10						7	3
	Mweni	4					1	3	
	Mooi	9						9	
Umgeni	Krantzkloof	6						2	4
		93				2	10	63	18

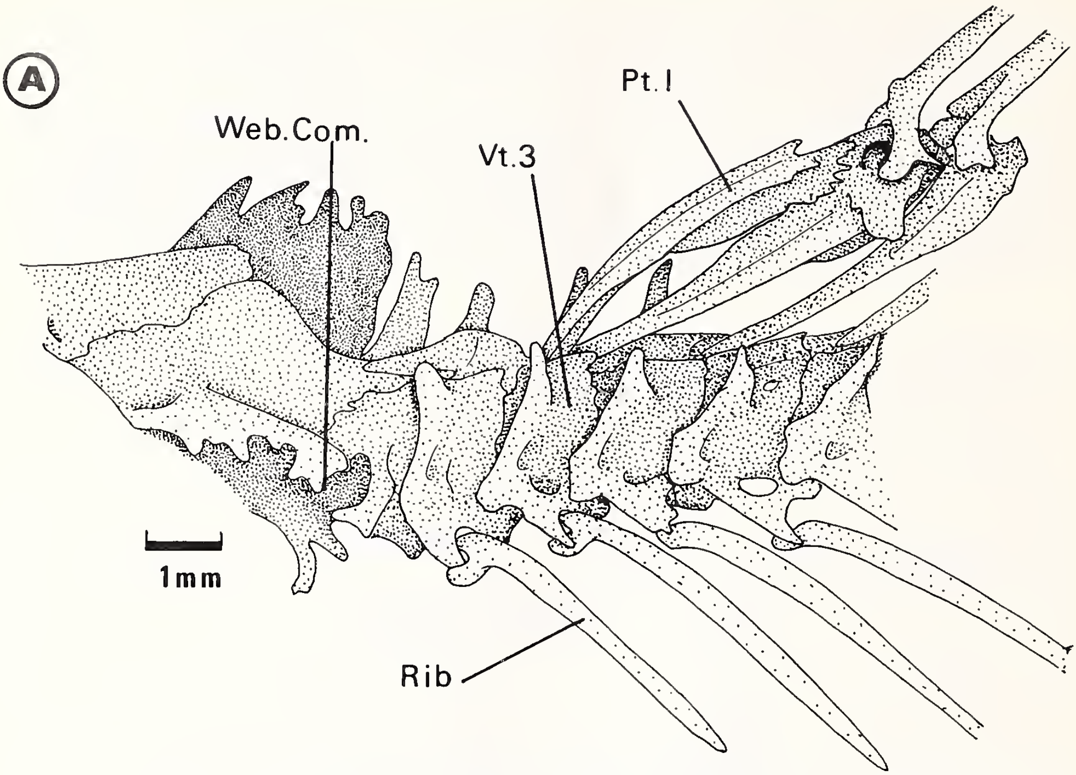
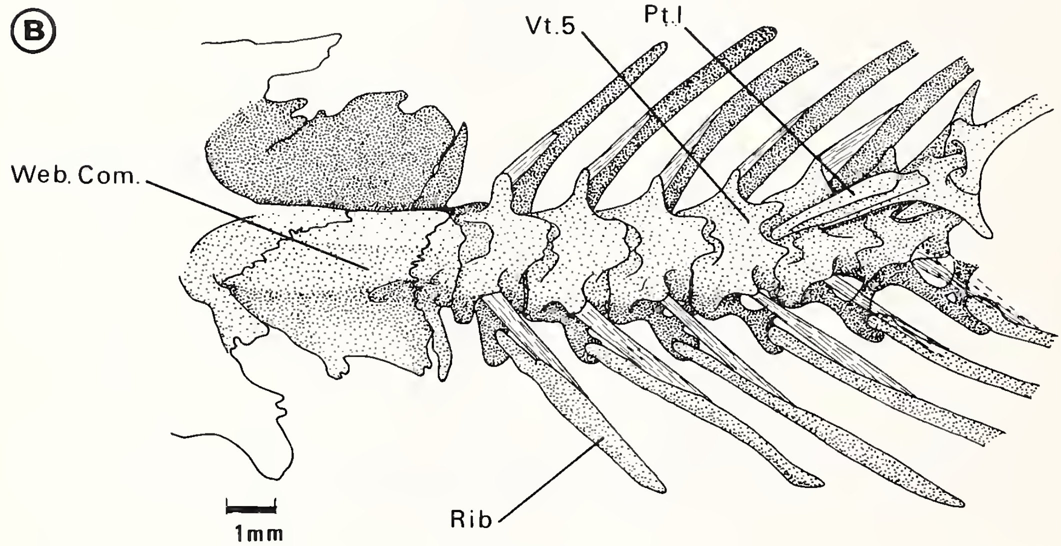


Fig. 14. A) Lateral view of portion of the skeleton of *A. uranoscopus* (AMSA/P 672) in the region between the head and the dorsal fin.



B) Latero-dorsal view of portion of the skeleton of *A. natalensis* (AMSA/P 895) in the region between the head and the dorsal fin.

TABLE 5

Distribution frequency of vertebral counts of *Amphilius* species in southern Africa. (Counts exclude 1–4 Weberian vertebrae).

A.	*Total Vertebrae*	N	36	37	38	39	40	
	A. natalensis	93	6	27	28	27	5	
	A. uranoscopus	109	9	37	42	20	1	
B.	*Precaudal Vertebrae*	N	15	16	17	18		
	A. natalensis	93	13	42	31	7		
	A. uranoscopus	109	3	54	48	4		
C.	*Caudal Vertebrae*	N	19	20	21	22	23	24
	A. natalensis	93		6	41	40	5	1
	A. uranoscopus	109	1	16	60	25	7	
D.	*Pre-anal Vertebrae*	N	20	21	22	23	24	
	A. natalensis	93	5	27	46	14	1	
	A. uranoscopus	109	12	46	44	7		

There are no clear differences in other vertebral meristic characters (Table 5A-D) between the two species. The pattern of hypural fusion in the caudal skeleton (Table 6A, B) indicates a wide variation for both species and a certain degree of overlap. The variation is more marked for *A. uranoscopus* in which a maximum of 26,7% of the specimens examined had any one particular pattern of hypural fusion (ph − 1 + 2 − 3 + 4 − 5 + 6). By contrast 63,5% of *A. natalensis* specimens had the same pattern of hypural fusion (ph − 1 + 2 − 3 + 4 − 5 + 6). It is clearly evident from Table 6 that *A. natalensis* exhibits a much greater degree of fusion of the hypurals than does *A. uranoscopus*. Nearly all *A. natalensis* have the parhypural fused with hypurals one and two but only 35% of *A. uranoscopus* show this. *A. natalensis* consistently has a higher percentage frequency than *A. uranoscopus* for each element of hypural fusion considered independantly (Table 6B). Externally the caudal fin of *A. natalensis* is usually more deeply forked than that of *A. uranoscopus*, however, this is not consistent and cannot be used as a diagnostic feature.

The general osteology of the two species was also studied but, apart from those mentioned above, no trenchant differences have been detected.

Both *A. natalensis* and *A. uranoscopus* have a notoriously variable range of pigmentation (Jubb, 1967). This intraspecific variation can exist within or between populations in the same river system. Pigmentation patterns include a plain dark grey or brown with lighter 'saddles' before and behind the dorsal, adipose and caudal fins, or the same with fine, medium or large spots, or a marbled or mottled arrangement which itself can vary in contrast. Certain populations are reasonably characteristic in pigmentation e.g. the only population of *A. natalensis* in the Blyde River is uniform dark brown, almost black and all specimens of *A. uranoscopus* from the Kavango River are heavily mottled. As yet no correlation with habitat type is evident and indeed collections from single localities can show a large range of pigment form so that the possibility of any correlation seems doubtful.

TABLE 6

Intraspecific variation in caudal skeleton structure of *Amphilius uranoscopus* and *Amphilius natalensis* from southern Africa. (Ph – parhypural; + – fused, – not fused, hypural bones numbered 1 to 6 from ventral to dorsal).

A. FREQUENCY OF PATTERN OF HYDURAL FUSION

	N	Ph−1+2−3−4−5−6	Ph−1+2−3+4−5−6	Ph−1+2−3+4−5+6	Ph−1+2−3−4−5+6	Ph+1+2−3−4−5−6	Ph+1+2−3+4−5−6	Ph+1+2−3+4−5+6	Ph+1+2−3−4−5+6	Ph+1+2+3+4+5+6
A. uranoscopus	60	9	16	4	10	4	13	2	2	
% frequency		15	26,7	6,7	16,7	6,7	21,7	3,3	3,3	
A. natalensis	63			1		1	12	40	6	3
% frequency				1,6		1,6	19	63,5	9,5	4,8

B. Degree of fusion of hypural elements in the caudal skeleton of *A. uranoscopus* and *A. natalensis* from southern Africa.

HYPURAL PATTERN

	N	Ph−1+2	Ph+1+2	3−4	3+4	5−6	5+6
A. uranoscopus	60	39	21	25	35	42	18
%frequency		65	35	41,6	58,3	70	30
A. natalensis	63	1	62	7	56	13	50
% frequency		1,6	98,4	11,1	88,9	20,6	79,4

COMMENTS ON THE TAXONOMIC STATUS OF *A. LAMPEI*, *A. NATALENSIS* AND RELATED SPECIES

The conclusion reached above on the status of the Nyazengu *Amphilius* immediately raises the question of the taxonomic status of *A. natalensis* Boulenger and *A. lampei* Pietschmann. Examination of the only available paratype of *A. lampei* (NMW 48094; Fig. 4) provides a basis for answering this question. *A. lampei* was described from two specimens both originally in the

Wiesbaden Museum (Pietschmann, 1913). Neither of these specimens was found, when requested for this study, and they were presumed lost in World War II (Dr R. Mentzel *in litt*). Fortunately the paratype appears to have been sent to the Vienna Natural History Museum before the war and was found there during a visit by the author in September 1981.

Several proportional measurements of the *A. lampei* paratype and the 'topotypes' of *A. natalensis* do not exactly coincide (Table 7) but are comparably similar considering the few specimens in either sample. Indeed in several characters, for which a large number of specimens of *A. natalensis* was measured (for comparison with *A. uranoscopus* in previous section), the range easily encompasses that of the paratype of *A. lampei*. Differences, such as in the number of preanal vertebrae, are difficult to evaluate conclusively from the single paratype. As the two samples were taken from the extremes in the distribution of this species a few differences of this sort were to be expected. 'Handling' the type specimen of *A. lampei* and a wide range of *A. natalensis* specimens certainly leaves little doubt that they belong to the same morphological species.

The most northerly locality from which *A. natalensis* has been recorded is the Ruo River in Malaŵi (BMH 1978. 12.13: 13–14). The problem of the enormous geographical gap between this and the type locality of *A. lampei* in Ethiopia (Fig. 3) is not really answerable without considerably more detailed collections from the intervening rivers. The possibility of other known species within this range being synonymous has also been investigated. Based on the combined criteria of predorsal vertebrae and the number of caudal fin rays (8 + 9; see above 'identity of *A. platychir*') only one species, *A. kivuensis* Pellegrin 1933 is a possible candidate. The proportional measurements of three of the type specimens are given in Table 7 for comparison with those of the type of *A. lampei* and of topotypes of *A. natalensis*.

It is evident that there is a general morphometric similarity between the specimens in Table 7. The *A. kivuensis* types differ slightly in having a longer and broader head, shorter orbit diameter and longer postorbit than either *A. lempei* or *A. natalensis*. In the vertebral column *A. kivuensis* has a relatively high count which is reflected to some degree in both the precaudal and caudal counts. The differences are nevertheless not distinctive. In the caudal skeleton *A. kivuensis* differs in not having hypurals five and six fused. Poll (1953) and Brichard (1978) remark that the caudal fin is straight (i.e. truncate), rather than notched, in this species. Once again the data from the type specimens suggest that they belong to a single variable species. A formal synonymy is not proposed before a larger series of *A. kivuensis* specimens can be examined in detail.

The discovery of *A. natalensis* in the Ruo River requires a re-examination of the identity of *A. hargeri* Boulenger (1907) from this site. Barnard (1942) speculated that "*A. natalensis* could quite possibly be linked with the two Nyasaland species *A. platychir* and *A. hargeri*". However, this was before the southern African species were well known. Jubb (1967) and Bell-Cross (1973) considered *A. hargeri* to be a junior synonym of *A. platychir* (= *A. uranoscopus*) without apparently examining the type of the species. The single type of *A. hargeri* (Table 2) does not provide an absolute answer to the problem. In most measurements and characters the specimen agrees more closely with *A. uranoscopus* (*sensu lato*) than with *A. natalensis*. However, the head length to length from head to dorsal fin ratio is 1,35, much nearer the value given by Crass (1964) for *A. natalensis* (1,1–1,3) than to *A. platychir* (= *A. uranoscopus*) (1,6–2,0). The first dorsal pterygiophore intercepts the third post-Weberian vertebrum. Although pigmentation is a variable character, all *A. natalensis* examined have the lighter 'saddles' before and behind the dorsal fins as described for the type of *A. hargeri*. The caudal skeleton of *A. hargeri* is of a type unusual for *A. natalensis* as it is relatively unconsolidated. In this respect, a higher percentage of the *A. uranoscopus* featured the same pattern as *A. hargeri*. *A. natalensis* has been found in the Ruo River, however, only in the uppermost reaches (D. Tweddle pers. comm.). The ambiguous character of the type specimen of *A. hargeri* sug-

TABLE 7

Comparison of morphometric and meristic characters of the types of *Amphilius lampei* Pietschmann, *A. kivuensis* Pellegrin and topotypes of *Amphilius natalensis* Blgr.

CHARACTER	*A. lampei* (N=1)	*A. kivuensis* $\overline{M}$	(N=3) Range	*A. natalensis* $\overline{M}$	(N=6) Range
Measurements					
Standard length (mm)	76,0		60,0–88,0		47,0 – 74,7
As % Standard length					
Predorsal length	37,5	40,3	39,8–41,0	40,0	38,7 – 41,1
Head length	20,3	23,0	22,0–24,3	20,5	20,1 – 20,9
Head depth	10,5	11,8	11,3–12,5	11,7	10,6 – 13,6
Head width	17,5	21,7	20,5–23,1	19,3	18,1 – 20,4
Head length/Head to Dorsal (Not % SL)	11,3			10,4	0,94– 1,09
Body depth	13,9	14,3	13,0–15,6	13,8	12,3 – 15,4
Body width	15,1	16,1	15,8–16,5	14,8	14,0 – 15,8
Caudal pedunele length	21,7	19,2	17,8–20,5	19,4	18,2 – 21,3
Caudal peduncle depth	11,6	10,8	10,3–11,4	9,7	9,4 – 10,2
Dorsal fin length	17,4	18,9	18,7–19,3	19,7	17,5 – 21,3
Anal fin length	17,4	17,9	17,6–18,3	16,6	16,0 – 17,1
Pectoral fin length	19,7	20,8	20,5–21,1	21,5	19,8 – 22,3
Pelvic fin length	18,4	18,1	17,5–18,8	18,6	18,1 – 19,7
As % Head length					
Snout	53,2	49,1	46,6–52,9	55,8	51,1 – 61,3
Orbit	13,0	10,3	9,1–11,5	14,0	11,7 – 16,4
Interorbit	29,9	30,8	28,4–33,3	33,3	30,7 – 36,5
Postorbit	41,6	46,8	41,1–49,7	39,2	36,5 – 40,9
Maxillary barbel	58,4	94,4	83,6–100,9	94,2	84,5 –103,3
Mandibular barbel (inner)	39,0	39,2	30,8–43,6	33,9	26,6 – 38,7
Mandibular barbel (outer)	55,2	72,8	66,4–72,2	57,5	54,0 – 60,5
As % Snout length					
Orbit-post. nare	35,4	40,6	36,8–46,8	40,1	37,5 – 45,0
Post, nare-ant. nare	30,5	24,7	22,7–27,8	28,4	23,7 – 30,0
Ant. nare-mid snout	43,9	41,8	39,7–45,6	40,3	34,3 – 44,7
Fin Rays					
Dorsal fin	i,6	i,6(3)		i,6(6)	
Anal fin	iii,6	ii,6(3)		iii,5(4); iii,6(2)	
Pectoral fin	1,10	1,9(3)		1,9(6)	
Pelvic fin	1,5	1,5(3)		1,5(6)	
Caudal fin	8 + 9	8 + 9(3)		8 + 9(6)	
Gill rakers (Ant. arch)	1 + 5	2 – 3 + 4 – 5		1 – 3 + 3 – 4	
Vertebrae					
Total vertebrae*	38	39(3), 40(5)		37(1), 38(4), 39(1)	
Precaudal vertebrae*	16	17(6), 18(2)		15(1), 16(2), 17(3)	
Caudal vertebrae*	22	22(6), 23(2)		21(2), 22(4)	
Predorsal vertebrae*	5	3(1), 4(4), 5(3)		5(2), 6(4)	
Preanal vertebrae*	20	22(5), 23(3)		21(1), 22(3), 23(1), 24(1)	
Hypural pattern	Ph + 1 + 2 – 3 – 4 – 5 + 6	Ph – 1 + 2 – 3 – 4 – 5 – 6(1) Ph – 1 + 2 – 3 + 4 – 5 – 6(2)		Ph + 1 + 2 – 3 – 4 – 5 + 6(2) Ph + 1 + 2 – 3 + 4 – 5 + 6(2)	

*Vertebral count exclude 1–4 Weberian vertebrae.

gests it is not from the population from the upper reaches of the river. It may represent a hybrid specimen but is best considered a junior synonym of *A. uranoscopus*.

The study of the type specimens of these widely scattered nominal species suggests that a single widespread species is present. However, it would not be wise to formally unite all these nominal species until the limits of variation of the parent populations, and possibly intermediate populations as for the Zambezi southwards, are better known. For the present three closely similar and possibly related species are therefore recognized, *A. lampei* in the Webi Shebeli system, *A. kivuensis* around Lake Kivu and northern Lake Tanganyika and *A. natalensis* from tributaries of the Zambezi southwards to the Umkomaas River in Natal.

The pattern of distribution of these species is interesting in that it conforms to the archipelago-like pattern of the Afro-montane Region (White, 1978) and outliers of the Capensis Region (Taylor, 1978). The distributions of several other unrelated fish species or species groups in southern Africa are also known to agree with this pattern. The pattern has been well exposed for various invertebrates (Stückenberg, 1962) amphibians and reptiles (Poynton, 1964; Poynton & Broadley, 1978), birds (Moreau, 1966; Hall & Moreau, 1970) and possibly even mammals (Delaney & Happold, 1979). The basic idea offered to explain this distribution has been that these are refugia which expand and contract their range under long-term climatic fluctuations. The result is a recurrent merging and isolation of the ecozones allowing the flora and fauna to colonize a much wider range than the present restricted areas around high mountains and mountain belts. Freshwater fishes that agree with this pattern are riverine species favouring headwater environments. Presumably these situations are those most likely to undergo catchment transfers through river piracies, especially during pluvial periods, which could provide the effective means for attaining such wide distribution ranges as witnessed for *A. natalensis, A. kivuensis* and *A. lampei.*

DESCRIPTION OF A NEW *AMPHILIUS* SPECIES FROM THE BUZI RIVER

Amphilius laticaudatus **sp. nov.**
Buzi River catlet. Figs 15, 16, 17.

Holotype: AMSA/P 5815 ♀ 51,5 mm SL. Buzi River at bridge on Inchope to Lourenco Marques road, Mocambique, 19° 55′S, 34° 15′E. Collector, G. Bell-Cross, 6 August 1972.

Paratypes: 2, AMSA/P 5816 ♀ 50,5 mm SL, ♂ 24,6 mm SL. 19 km above new Revue River bridge, Revue River, Buzi River system, Mocambique. 19° 10′S, 33° 15′E. Collector, G. Bell-Cross, 15 August 1972.

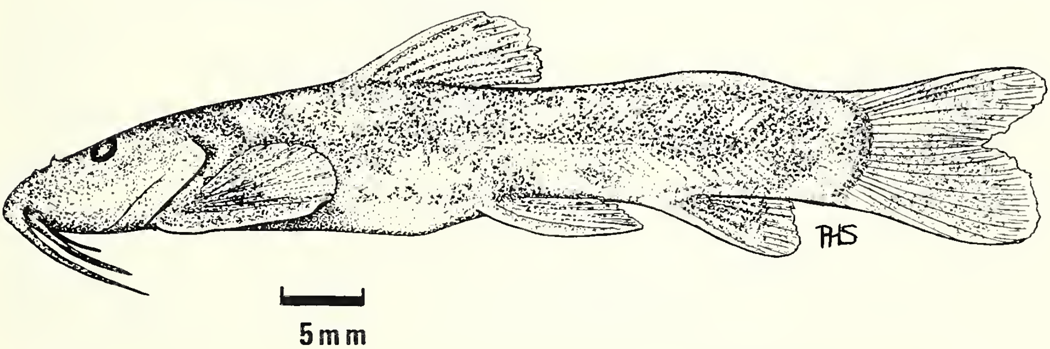


Fig. 15. Lateral view of holotype of *Amphilius laticaudatus* (sp. nov.) AMSA/P 5815; SL = 51,5 mm ♀.

Diagnosis

A small *Amphilius* species (maximum length recorded, 51,5 mm SL) with morphometric proportions and meristic characters as recorded in Table 8. Head flat below, convex above and bluntly rounded anteriorly. Head 3,8 to 4,1 ($\overline{\mathrm{M}4}$) ($\bar{x} = 4$) times in SL, entirely covered with fleshy skin. Angle of lateral profile shallow (20–30°), rising in gentle arch to dorsal fin. Eyes dorso-lateral without free orbit and widely spaced. Nares widely separate, anterior rounded short tubular, posterior oval with fleshy ridge, located approximately in mid-third of snout. Mouth sub-terminal, gently curved (almost straight) and broad (about half total width of head). Lips moderately fleshy. Three pairs of simple tapered circum-oral barbels (Fig. 16), maxillaries extending laterally from upper jaw reaching to anterior base of pectoral fin; outer mandibulars extend from lateral angle of mouth reaching anterior base of pectoral fin; inner mandibulars with base directly medial to outer pair, not reaching posterior edge of branchiostegal membrane (Fig. 16). Branchiostegal membrane free, continuous but deeply notched mid-ventrally.

Body sub-oval anteriorly, flattened below from between pectoral fins to anal region behind pelvic fins, increasingly compressed from behind pelvics to caudal peduncle. Caudal pe-

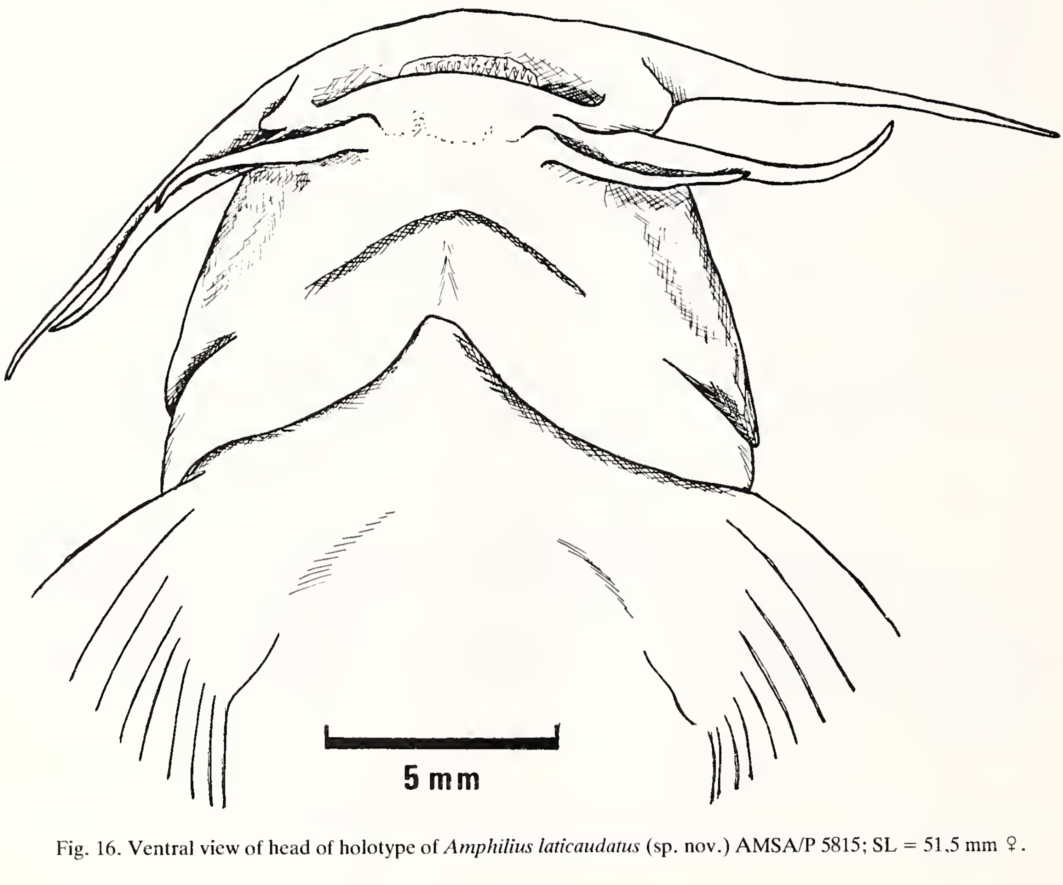


Fig. 16. Ventral view of head of holotype of *Amphilius laticaudatus* (sp. nov.) AMSA/P 5815; SL = 51,5 mm ♀.

TABLE 8

Morphometric and meristic measurements of the type specimens of *Amphilius laticaudatus*

HT — Holotype

Measurement	Mean	Range	(HT)
Standard length		24,6 –51,5	51,5
As % Standard length			
Predorsal length	44,0	43,1 –44,7	44,3
Head length	24,8	24,1 –26,0	24,3
Head depth	13,8	12,9 –14,3	12,9
Head width	24,1	23,5 –24,4	23,5
Head — dorsal (H-D)	20,0	17,9 –21,4	21,4
Head length/Head to Dorsal (Not % SL)	1,25	1,13– 1,45	1,13
Body depth	16,5	15,0 –19,2	15,3
Body width	18,3	15,4 –20,0	19,6
Caudal peduncle length	16,8	16,7 –16,9	16,7
Caudal peduncle depth	13,5	12,9 –14,3	12,9
Dorsal fin	23,3	21,6 –26,0	22,4
Anal fin	18,5	17,1 –20,3	17,1
Pectoral fin	24,3	23,6 –24,9	24,5
Pelvic fin	20,9	19,9 –21,6	21,2
As % Head length			
Snout	52,0	51,6 –53,2	53,2
Orbit	16,0	14,1 –17,9	16,1
Interorbit	33,3	30,1 –35,9	33,9
Postorbit	41,0	37,4 –43,5	43,5
Maxillary barbel	75,7	72,6 –78,1	72,6
Mandibular barbel (inner)	41,9	35,9 –52,0	37,9
Mandibular barbel (outer)	56,2	48,8 –60,5	60,5
As % Snout length			
Orbit-post. nare	37,0	30,3 –40,9	40,9
Post. nare-ant. nare	34,8	28,6 –42,4	33,3
Ant. nare-mid tip	43,0	39,7 –48,5	40,9
Adipose fin	19,9	17,6 –22,4	19,6
Fin Rays			
Dorsal fin	1,6(3)		1,6
Anal fin	1,5; iii, 5; iii, 4		iii,4
Pectoral fin	1,9; 10(1)		1–10
Pelvic fin	1,5(3)		1,5
Caudal fin	8 + 9(3)		8 + 9
Gill rakers	1 – 2 + 3 – 4		2 + 4
Vertebrae			
Vertebrae	32(1), 33(1), 34(1)		32
Precaudal vertebrae	15(2), 16(1)		15
Caudal vertebrae	17(1), 18(2)		17
Predorsal vertebrae	3(1), 4(2)		3
Preanal vertebrae	19(2), 21(1)		19
Hypural pattern	Ph–1+2–3–4–5–6		Ph–1+2–3–4–5–6

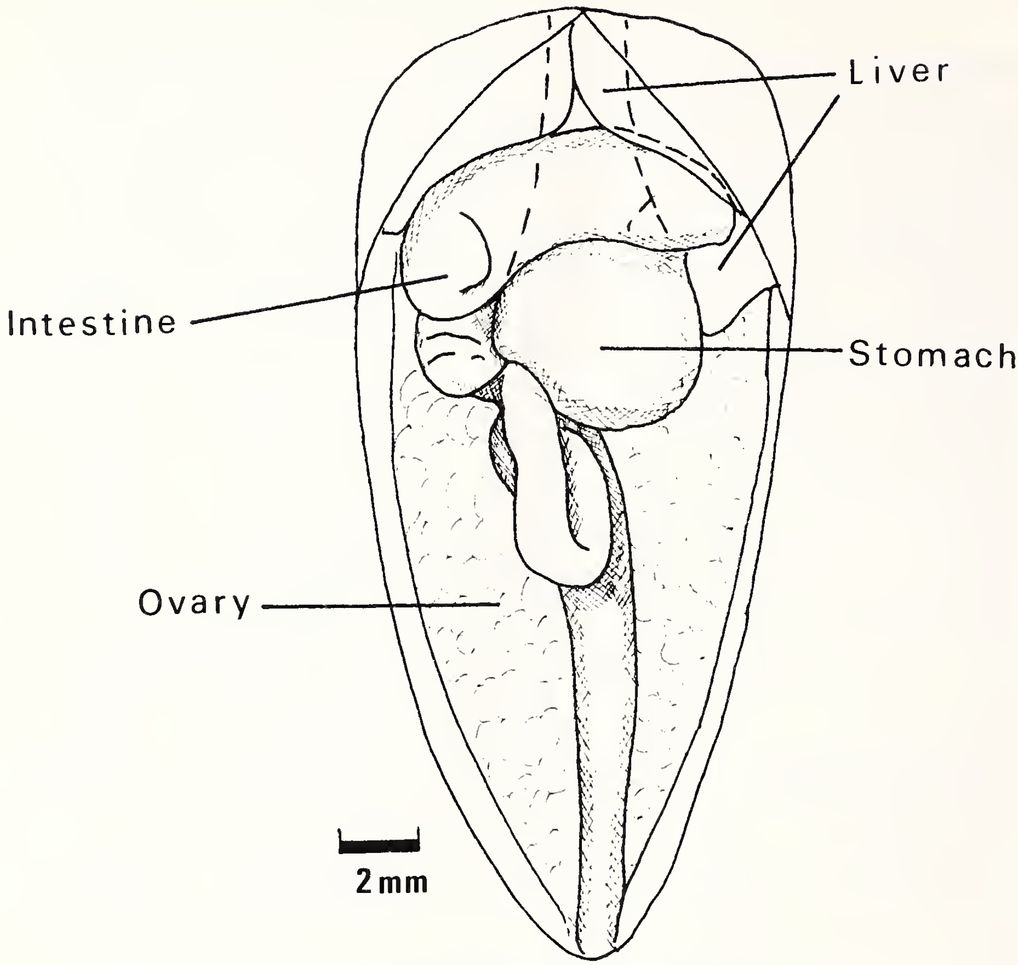


Fig. 17. Semi-diagrammatic view of alimentary canal *in situ* of paratype of *Amphilius laticaudatus*.

duncle short, 1,24 (1,18–1,29) times as long as deep. Anus located between pelvic, one quarter of distance from posterior edge of pelvic bases to anal fin. Skin smooth throughout.

Dorsal fin with rounded or straight posterior edge; simple leading ray segmented and flexible, slightly shorter than first branched ray. Origin of dorsal over hind margin of pectoral fins. Dorsal fin base entirely ahead of pelvic fins. Adipose dorsal fin low and smoothly confluent with caudal ridge. Pectoral fins large and rounded with outer rays horizontal and inner rays directed postero-dorsally against body. Leading ray expanded with fine filaments and covered by thick pad. Pelvics similarly expanded but smaller, inner rays in same horizontal plane as other rays of this fin. Leading ray expanded with fine filaments and covered by thick pad. Anal fin short with straight posterior edge. Caudal fin shallowly forked with rounded lobes.

Lateral line simple, straight, extending mid-laterally from head to posterior end of caudal peduncle. Teeth small, villiform, in broad bands on premaxillary and along ramus of lower jaw. Gill rakers long and slender, absent from posterior rim of first and second arches (in the holotype the second arch has a single raker on posterior edge of dorsal limb). Alimentary canal short, as illustrated in Fig. 17.

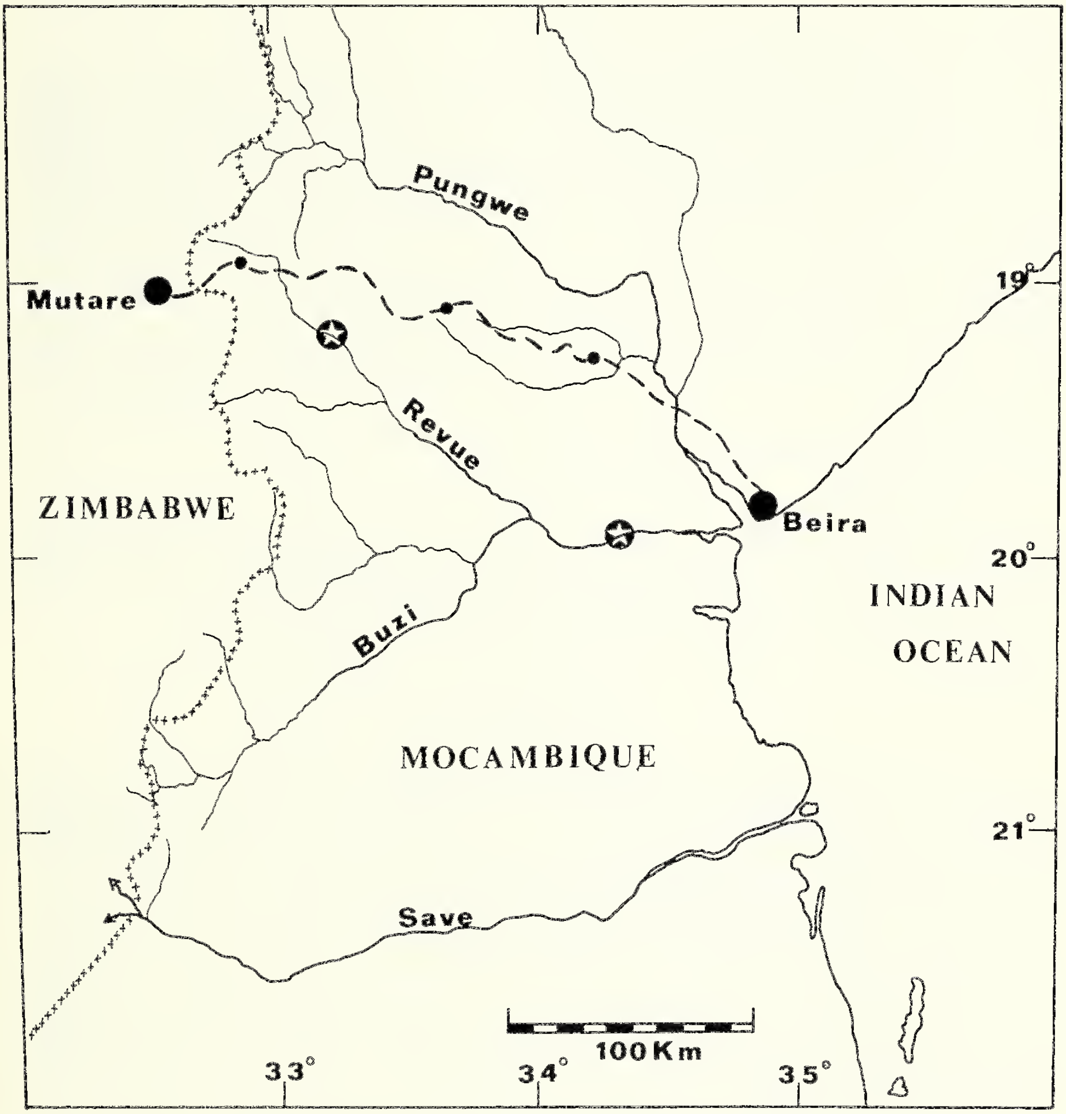


Fig. 18. Collecting sites ⊛ of *A. laticaudatus* in the Buzi River system.

Preserved colours mottled brown and cream, eyes black. Pigment pattern irregular and heavily mottled with speckled pigment clouds and three or four large cream saddles on dorsal surface, one over predorsal area, one behind base of dorsal fin, one over pre-adipose region and the fourth over the posterior portion of the adipose fin and adjacent body regions. Saddles bordered by broad dark band. Belly and ventral surfaces pale cream. Dark crescent along base of caudal fin. Fins mottled with brown pigment tending to form a band on dorsal and caudal fins.

Comparison with A. uranoscopus *and* A. natalensis

A. laticaudatus differs from both *A. uranoscopus* and *A. natalensis* in having fewer vertebrae, particularly fewer caudal vertebrae. It has a shorter, deeper caudal peduncle than either of these species and also a longer predorsal distance. The head is relatively large being longer, broader and deeper than that of *A. natalensis* and although only marginally longer and broader than that of *A. uranoscopus* it is relatively deeper. These proportions are also reflected in the body measurements. *A. laticaudatus* has a relatively large eye compared with either sympatric species. *A. laticaudatus* also differs from *A. natalensis* in having generally fewer predorsal and preanal vertebrae and a more deeply notched branchiostegal membrane. *A. natalensis* in the Buzi River has a similar adipose fin but differs in pigmentation as specimens of this species are generally a uniform dark brown with small pale dorsal 'saddles'. *A. uranoscopus* has a shorter head to dorsal distance and correspondingly fewer predorsal vertebrae than has *A. laticaudatus*. The eyes are smaller and more closely set and the nares further forward on the snout in *A. uranoscopus*.

The adipose fin in *A. uranoscopus* is notched behind to form a free edge and has not been seen to be confluent in any population examined.

Distribution and habitat

A. laticaudatus was collected from two sites within the Buzi system (Fig. 18). A description of the habitat at these localities was provided by the collector, Mr G. Bell-Cross: the collecting sites were all in fast flowing shallow water up to 0,5 m deep over rocks and pebbles. The predominant and usually solitary macrophyte was *Hydrostachys polymorpha*.

Etymology

Laticaudatus refers to the relatively short deep caudal peduncle of the new species.

DISCUSSION

Bell-Cross (1973) prepared a checklist of the ichthyofauna of Buzi River, but concluded that it was probably incomplete. This paper adds two *Amphilius* catfish species to that list. The Buzi system certainly is exceptional in regard to its fish fauna and warrants a great deal of further investigation. Study of its hydrographical history would be of great interest to zoogeographers and would help to unravel the questions of origin of its ichthyofauna.

At this stage there is little indication of the phyletic relationships of *Amphilius laticaudatus*. It shares certain plesiomorph characteristics (e.g. caudal fin rays) with other *Amphilius* sp. which merely suggest its broad group affinities with east and southern African *Amphilius* by excluding relationship with west African species. Similarities in pigmentation with certain *A. natalensis* populations (e.g. in the Ruo River, Malaŵi) are not supported by other more tangible characteristics and, besides, such similarity is also to be found in various populations of several widespread *Amphilius* species. Study of the skeleton of the species might indicate its relationships, but additional material would be required.

The question of the correct identity of *Amphilius brevidorsalis* Pellegrin has been reasonably solved by reference to the type specimen. It is definitely not a specimen of *A. laticaudatus*

nor of *A. natalensis* but agrees in the general characters with *A. uranoscopus* in all respects apart from the short dorsal fin. On its own the short dorsal fin (fewer rays) probably represents the extreme of natural variation or an isolated mutation and certainly does not require formal recognition of any kind.

SUMMARY

The paper considers the taxonomy of *Amphilius* species from east and southern Africa. It is clear that the widespread species of this region has been grossly misidentified as *A. platychir*, a species confined in reality to West Africa. The valid name for the widespread species of east and southern Africa is *A. uranoscopus*. A second species *A. natalensis* is found in tributaries of the lower Zambezi River southwards to Natal. It is similar to *A. kivuensis* from mountain streams around Lake Kivu and *A. lampei* from the mountains of Ethiopia. A new species of *Amphilius* is described, apparently confined to the Buzi River system of Mozambique.

An abbreviated synonymy of the species considered is as follows:

1. *Amphilius platychir* (Günther, 1864)

Synonyms: *Pimelodus platychir* Günther, 1864.
Amphilius platychir: only references to the species from West Africa.
Amphilius grammatophorus Pellegrin, 1913.

2. *Amphilius uranoscopus* (Pfeffer, 1889)

Synonyms: *Anoplopterus uranoscopus* Pfeffer, 1889.
Amphilius uranoscopus
Amphilius platychir: all references to this species from east central and southern Africa.
Amphilius platychir cubangoensis Pellegrin, 1936.
Chimarrhoglanis leroyi Vaillant, 1897.
Amphilius leroyi
Amphilius jacksoni David, 1937: 418.
Amphilius grandis Boulenger, 1905.
Amphilius transvaalensis (see note in Harry, 1953)
Amphilius hargeri Boulenger, 1907.
Amphilius kreffti Boulenger, 1911.
Amphilius oxyrhinus Boulenger, 1912.
Amphilius brevidorsalis Pellegrin, 1919.

3. *Amphilius lampei* Pietschmann, 1913.

4. *Amphilius natalensis* Boulenger, 1917.

Synonyms: *Amphilius longirostris* (*non* Boulenger) Gilchrist & Thompson, 1917: 558 Fig. 166
Amphilius lampei (*non* Pietschmann) Bell-Cross & Jubb, 1973: 4, Fig. 3.

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APPENDIX 1

Material measured and/or x-rayed (excluding types given in Table 1).

This appendix lists material specifically measured and/or x-rayed for this study. In addition the entire collection of *Amphilius* in the Albany Museum was examined and sorted according to the findings of the study. A complete list of this material is available on request. Material of these species in the British Museum (Natural History), Museum National d'Histoire Naturelle, Paris, and Museum Royale d'Afrique Centrale, Tervuren, was cursorily examined without measurement or being x-rayed.

ABBREVIATIONS

Amphilius uranoscopus

Reg. No.		Locality (River and System)	Collector	Date
AMSA/P	326	Marozi R. Zambezi	R. A. Jubb	04/1958
	506	Ruo R. Zambezi	G. Bell-Cross	12/1964
	672	Odzi R. Save	R. A. Jubb	05/1958
	718	Marozi R. Zambezi	R. A. Jubb	05/1958
	1219	Mhlambonyati R. Incomati		1968
	1990	Lundi R. Save	F. Junor	1963
	4235	Komati R. Incomati	I. Gaigher	05/1967
	4236	Noordkaap R. Incomati	I. Gaigher	04/1967
	4239	Elands R. Incomati	F. J. van der Merwe	09/1965
	4252	Komati R. Incomati	I. Gaigher	05/1967
	4255	Molapitsi R. Limpopo	F. J. van der Merwe	06/1965
	4258	Komati R. Incomati	F. J. van der Merwe	01/1966
	4270	Waterval R. Incomati	I. Gaigher	06/1968
	4276	Olifants R. Limpopo	F. J. van der Merwe	09/1965
	5083	Mooketsi R. Limpopo	I. Gaigher	05/1968
	5120	Pongola	R. McC. Pott	06/1967
	5196	Pivaan R. Pongola	R. McC. Pott	06/1967
	5199	Assegaai R. Pongola	R. McC. Pott	06/1967
	5216	Usutu R. Pongola	R. McC. Pott	06/1967
	5304	Levubu R. Limpopo	I. Gaigher	07/1968
	5439	Ngwempisi R. Pongola	R. McC. Pott	06/1967
	5631	Okavango R.	B. v. d. Waal	11/1977
	5664	Okavango R.	B. v. d. Waal	11/1977
	5730	Okavango R.	B. v. d. Waal	11/1977
	5814 (in part)	Pungwe R.	G. Bell-Cross	06/1972
	5896	Ngwempisi R. Pongola	R. McC. Pott	06/1967
	6178	Usutu R. Pongola	R. McC. Pott	07/1967
	6188	Usutu R. Pongola	R. McC. Pott	07/1967
	7120	Spekboom R. Limpopo	I. Gaigher	05/1968
	7134	Treur R. Limpopo	Provincial Fish Inst.	
	7250	Mogol R. Limpopo	C. J. Kleynhans	09/1979
	7550	Ndzelele R. Limpopo	C. J. Kleynhans	12/1979
	7785	Letsitele R. Limpopo	C. J. Kleynhans	09/1980
QVM	2922 (in part)	Mtarazi R. Pungwe	I. Thompson	12/1972

Amphilius natalensis

Reg. No.	Locality (River and System)	Collector	Date
AMSA/P 326	Marozi R. Zambezi	R. A. Jubb	04/1958
680	Marozi R. Zambezi	R. A. Jubb	05/1958
714	Pungwe R.	National Museum Rhodesia	11/1957
718	Marozi R. Zambezi	R. A. Jubb	05/1958
863	Inyamvubu R. Tugela	Natal Parks Board	08/1964
895	Otimati R. Tugela	F. Farquharson	04/1964
1193	Ngwempisi R. Pongola	R. McC. Pott	1969
1198	Sand R. Incomati	I. Gaigher	1968
1285	Pungwe R.	D. C. H. Plowes	08/1965
1618	Lunsklip R. Incomati	I. Gaigher	1967
2094	Tugela R.	F. Farquharson	
2112	Nyazengu R. Pungwe	G. Bell-Cross	06/1972
3761	Blyde R. Limpopo	P. le Roux	06/1967
4277	Crocodile R. Incomati	F. J. van der Merwe	09/1965
4328	Tugela R.	R. Crass	
4336	Nyazengu R. Pungwe	G. Bell-Cross	06/1972
5110 (in part)	Assegaai R. Pongola	R. McC. Pott	06/1967
5814	Pungwe R.	G. Bell-Cross	06/1972
5815 (in part)	Buzi R.	G. Bell-Cross	08/1972
5816	Buzi R.	G. Bell-Cross	08/1972
7105	Hlelo R. Pongola	R. McC. Pott	06/1967
7291	Blyde R. Limpopo	C. J. Kleynhans	11/1978
8644	Soada R. Umkomaas	O. Bourquin	11/1981
9557	Krantzkloof R. Umgeni	R. Crass	11/1958
9558	Mweni R. Tugela	M. Coke	10/1968
9562	Ingogo R. Tugela	M. Coke	02/1964
QVM 2922	Mtarazi R. Pungwe	I. Thompson	12/1972
BMNH 1978 12.13: 13–14	Ruo R. Zambezi	D. Tweddle/N. Willoughby	1978

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Editor
Dr F.W. GESS: 1978 –

The distribution and status of bats (Mammalia: Chiroptera) in the Cape Province

by

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CONTENTS

ABSTRACT

Distribution maps with notes on taxonomy, distribution and status, habits, food and breeding are presented for 29 species of bats occurring in the Cape Province of the Republic of South Africa. Comparisons are made between data from the survey, which lasted from 1976 to 1979, and specimens examined in South African museums. The main motivation for the survey was the conservation of bats. A high priority was placed on collecting from roosts. Some very scarce and endemic species were collected and many interesting new localities were recorded.

UITTREKSEL

Verspreidingskaarte met aantekeninge oor die taksonomie, verspreiding en status, gewoontes, voedsel en aanteel van 29 species vlermuise wat in die Kaapprovinsie van die Republiek van Suid-Afrika voorkom, word aangebied. Vergelykings word gemaak tussen gegewens wat versamel is tydens die intensiewe opname, wat vanaf 1976 tot 1979 geduur het, en monsters wat bestudeer is in die groter Suid-Afrikaanse museums. Die motivering vir die opname was die bewaring van vlermuise, en 'n hoë voorkeur is geplaas op die versameling van data in die skuilplekke van elke spesie. Sommige van die baie skaars en endemiese spesies is versamel, en interessante nuwe voorkoms lokaliteite is gevind.

INTRODUCTION

In their identification manual for African Chiroptera Hayman & Hill (1971) express the opinion that there is unlimited scope for further work on practically every aspect of African bat systematics and biology. Up to now very little more than incidental collecting has been done in the Cape Province. Although naturalists such as Roberts, Shortridge and Allen collected much material and made substantial contributions to bat taxonomy, little information on their ecology is available.

The only attempt at an ecological study in the Cape Province was made between 1960 and 1963 when approximately 500 cave bats of the species *Rhinolophus capensis, Rhinolophus clivosus, Miniopterus schreibersii* and *Nycteris thebaica* were banded at De Hoop cave, Koegelbeen cave and at Die Oog (Kuruman) by B. Copley, Q. Siegrist and C. Gow, according to information from the Transvaal Museum bat banding project. Unfortunately there was no follow-up and therefore no information on the migration and longevity of the species was collected.

The present project was initiated to provide basic information on the conservation status of this large group of mammals and to draw attention to the important role that bats are likely to play in the natural ecosystems of the Cape Province. Whereas the frugivorous species are essential in nature as seed propagators, the insectivorous species are of considerable economic importance in the control of nocturnal insect populations. According to Davis *et al.* (1962) the free-tailed bats of Texas are capable of destroying 6 600 tons of insects yearly. Similarly, Dwyer (1964) calculated that *Miniopterus schreibersii* destroy about 200 pounds of insects per night in the Macleay Valley in Australia. At the second International Bat Research Conference held in Amsterdam in 1970 delegates from 20 countries agreed that the numbers of almost all bat species are declining, and that further research on the ecology of most species is essential for their survival (Stebbings 1970). The main reasons for the decline in numbers were listed as the effect of insecticides, lost habitat and unnecessary slaughter. They concluded that several species around the world are already endangered.

To draw up an effective conservation plan for bats it is necessary to find out their distribution and numbers, and to have a basic understanding of their roosting behaviour and seasonal movements. It was decided to start by concentrating on those species which congregate in large communal roosts, since these would be the easiest places to apply active conservation management. This paper reports on data on the status and distribution of all bats that were accumulated during field work, and more detailed information on population dynamics and migrations in some of the larger roosts will be reported elsewhere.

Most recent studies on the regional distribution of mammals in southern Africa include generalized and somewhat repetitive summaries of what is known of the biology of each bat species. Therefore the biological notes included here are mostly restricted to data collected during the study or else information in the literature that refers particularly to bats in the Cape Province.

The survey was carried out over the whole of the Cape Province (Fig. 1), an area of 641 500 km^2. All previous checklists on the mammals of South Africa were written with the inclusion of Transkei, Bophuthatswana and East Griqualand (the remainder of the Cape Province to the east of Transkei) in the Cape Province. However, these areas were excluded from the present study because the first two are now independent states and East Griqualand has been transferred to the province of Natal.

SURVEY METHODS

The first priority was to gather information on bat roosts. For this an intensive press campaign was carried out. In addition, letters of inquiry were sent to selected high schools and individuals, yielding information on localities of about 120 roosts. The field survey started during the winter of 1976 and lasted until the end of 1979. During this period several additional localities were found.

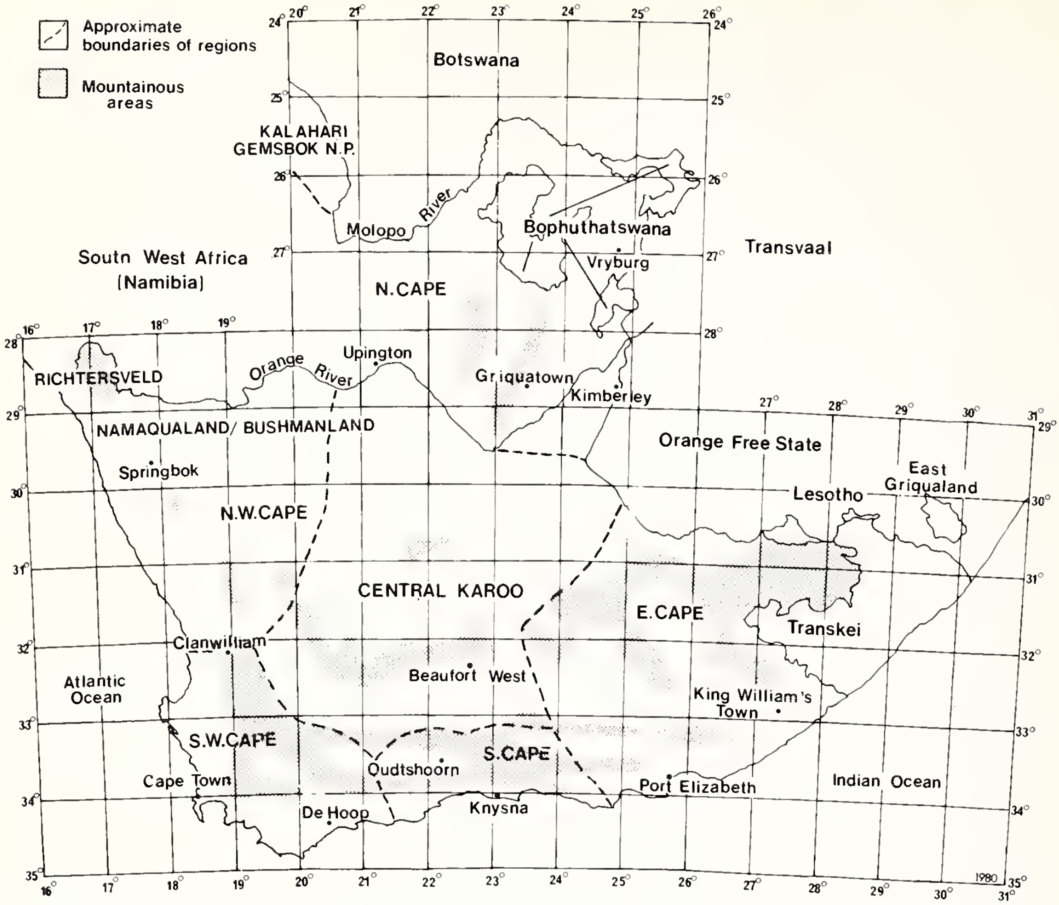

Fig. 1. Principal regions of the Cape Province.

As some species undertake seasonal migrations each roost was visited twice, the visits being in different seasons. Except for observations on nocturnal behaviour all visits were made during daylight. For safety at least two people entered the roosts at a time, and each wore a mine-torch, helmet and boots. To keep disturbance to a minimum the stay inside the roost was limited to not more than one hour.

During each visit notes on the numbers of each species in the population, the amount of guano, recaptures of banded bats, depth of the cave or mine, habits, temperature and humidity were recorded on field data sheets. A small sample of up to 20 bats of each species was taken with a hand-net, the size of the sample depending on the number in the population. Where roosts were too dangerous to enter, or where the openings were too small, mist-net samples were taken during the evenings at the time of emergence. On windy evenings, when the effectiveness of mist-nets was low, bats were shot on emergence with a .22 rifle loaded with dust-shot.

It soon became apparent that the scarcer species would be overlooked, if collecting at roosts was the only sampling method used, and mist-nets were therefore erected over reservoirs or streams in suitable areas. The nets were manned for at least five hours per night, starting from sunset, and bats were taken from the net at hourly intervals. Although this method yielded little information on the status of the species caught, it was useful for recording occurrence. In many areas, especially in the drier parts of the north-western Cape, up to 20 bats of five different species were caught per night.

At the De Hoop Cave, where the more intensive population study was carried out, a variation of the Tuttle-trap (Constantine 1956, Tuttle 1973) was used for catching the bats. At this site nearly 8 000 individuals of *Miniopterus schreibersii, Myotis tricolor, Rhinolophus clivosus* and *Rhinolophus capensis* were banded for the purpose of studying migration (Herselman & Norton in prep.) and population dynamics.

Bats to be prepared as museum specimens were killed with chloroform, fixed for 24 hours in 5% formalin, and preserved in 70% ethyl alcohol. Pregnant females were dissected to free the embryo for growth studies. The old preservative was replaced with a new solution every six months.

All the specimens collected were catalogued in the laboratory using the first three letters of the genus name and a three-digit number from 001 to 999 followed by the letter "J" (for Jonkershoek). For example, the fiftieth collected specimen of *Nycteris thebaica* would be catalogued as NYC 050 J. The identification of most of the material was carried out by the senior author, using descriptions and keys in Roberts (1951), Ellerman *et al.* (1953) and Hayman & Hill (1971). On a few occasions material was sent to Dr I. L. Rautenbach of the Transvaal Museum and to Prof J. Meester of the University of Natal. The entire collection of more than a thousand specimens of 19 species has been deposited in the Kaffrarian Museum in King William's Town.

During the study the Transvaal Museum in Pretoria, the Kaffrarian Museum in King William's Town, the Albany Museum in Grahamstown, and the South African Museum in Cape Town were visited to examine their bat material from the Cape Province. The authors are not aware of any other significant collections from this region and hope that these four collections contain the majority of bat specimens from the Cape Province available in South Africa.

A gazatteer was drawn up for all survey and museum specimens (Appendix). For survey material most spot localities were plotted to the nearest minute, whereas localities of museum specimens could seldom be recorded more accurately than the quarter degree grid square.

The distribution of survey sampling sites is shown in Fig 2. Localities of both survey and museum records were plotted on the maps using quarter degree squares and localities of special importance mentioned in the literature are indicated by an "S". To bring the distribution of each species into perspective a small map of Africa showing the approximate distribution range was drawn from information in Hayman & Hill (1971), Kingdon (1974) and Smithers (1983).

The text for each species includes a summary of the material examined, with the number of specimens and the localities where they were collected. Museum records are identified as follows: (TM) for the Transvaal Museum in Pretoria, (KWT) for the Kaffrarian Museum in King William's Town, (SAM) for the South African Museum in Cape Town, and (AM) for the Albany Museum in Grahamstown.

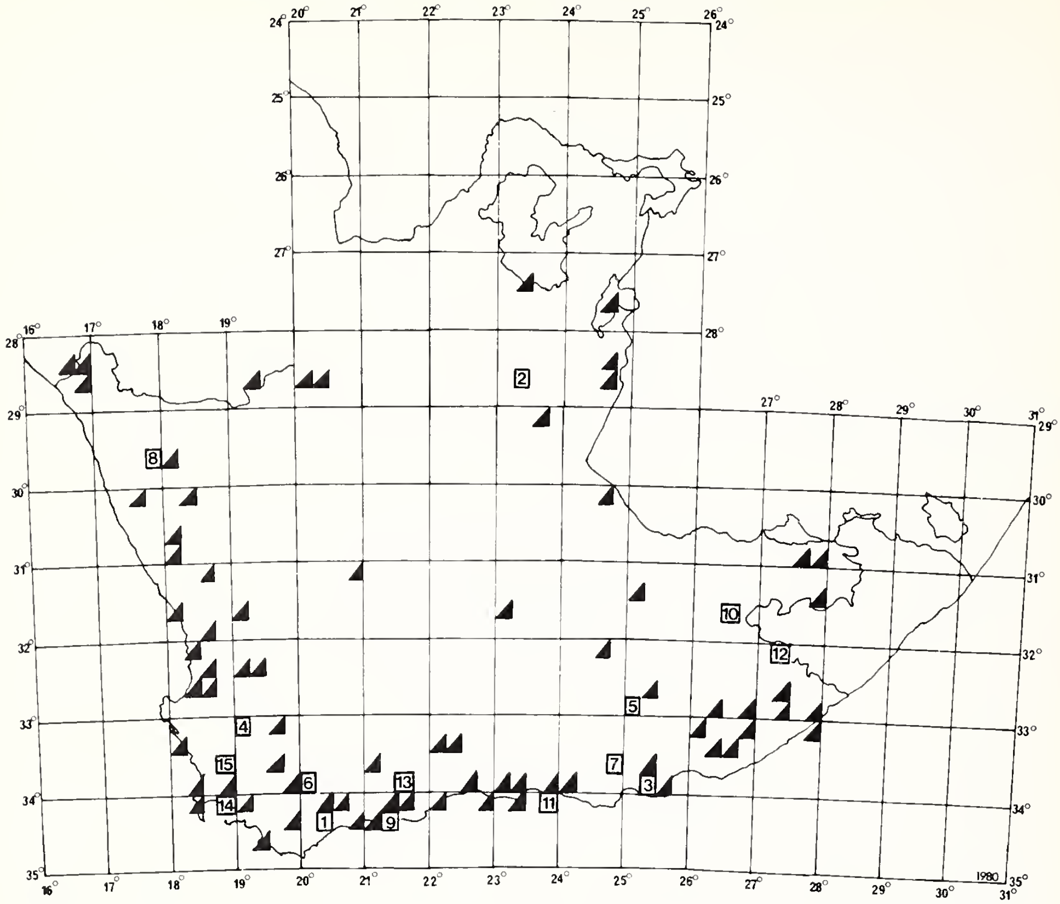

Fig. 2. Localities where bats were collected in the Cape Province. Numbers indicate major roosts listed in Table 2.

The order and taxonomy of all species follows that of Hayman & Hill (1971), with corrections and up-dating according to Swanepoel *et al.* (1980).

At the start of the survey the authors traced approximately 900 bat specimens from the Cape Province that had been deposited in South African museums, representing 23 of the 30 species then recorded in the Province. The collection with the largest number of specimens (440) was in the Kaffrarian Museum at King William's Town. A large number of specimens is also housed in museums overseas, including many type specimens, but these are not easily accessible for taxonomic and distributional study in this country.

The present survey yielded more than a thousand specimens of 21 species, which represents a substantial addition to the museum material available in the Cape Province. Nearly all of these specimens have been sent to the Kaffrarian Museum. The specimens were collected from localities distributed throughout the Cape Province, however, sampling was concentrated

mostly in the mountainous areas of the province with caves and mines suitable for large roosts (Fig. 2).

DISTRIBUTION AND STATUS OF INDIVIDUAL TAXA; BIOLOGICAL NOTES

Suborder MEGACHIROPTERA: Family PTEROPODIDAE

Epomophorus wahlbergi (Sundevall, 1846) Wahlberg's Epauletted Fruit Bat

The genus *Epomophorus* is easily recognized by the tuft of white hair at the base of the ear. *E. wahlbergi* differs from all other species of the genus occurring in Africa in that it has only one well-developed post-dental palatal ridge, whereas the others have two (Hayman & Hill 1971). However, Meester *et al.* (1964) mention the possibility that *E. wahlbergi* may be a subspecies of *E. crypturus*.

Roberts (1951) gave a range of 80–86 mm for the forearm length of *E. wahlbergi*. The range for the seven specimens collected during this survey from three localities is 77,5–85,5 mm.

Distribution and status

Epomophorus is the most widespread of all African fruit bat genera (Hayman & Hill 1971). *E. wahlbergi* can be found in a large part of central, eastern and southern Africa. In the Cape Province its distribution seems to be limited to the south-eastern and eastern Cape (Fig. 3). A series of specimens was collected from Grahamstown by J. C. Greig and C. T. Stuart of this Department. The authors collected one specimen from Walmer and one from as far south as Keurbooms River. From discussion with various people in the eastern Cape it appears that the species is fairly common in the area.

Habits

This species seems to roost in trees and was never found in caves or mines. In Walmer the authors often saw them resting in pine and cypress trees where they uttered their characteristic pinging sound. They appeared to prefer soft fruits which they carried from the low fruit trees to feeding roosts in higher trees.

Material examined

Survey — 5 Grahamstown, 1 Keurbooms Reserve, 1 Walmer.

Museums — 2 Alice, 1 Balossi, 1 Bedford, 1 Blaney, 1 Gladstone, 51 King William's Town, 2 Peddie, 3 Pirie (KWT); 2 King William's Town, 14 Port St Johns, 1 Umtata (SAM); 1 Bedford, 30 Grahamstown, 2 King William's Town, 1 Pirie (AM).

Epomophorus crypturus Peters, 1852 Peters' Epauletted Fruit Bat

The single specimen of this species caught during the survey was separated from *E. wahlbergi* on the basis of the second post-dental palatal ridge, as well as on more general external features. However, this could not be confirmed because there are no Cape specimens in the South African museums. Roberts (1951) noted a marked difference in forearm length between the two species, with *E. crypturus* being considerably shorter, but Hayman & Hill (1971)

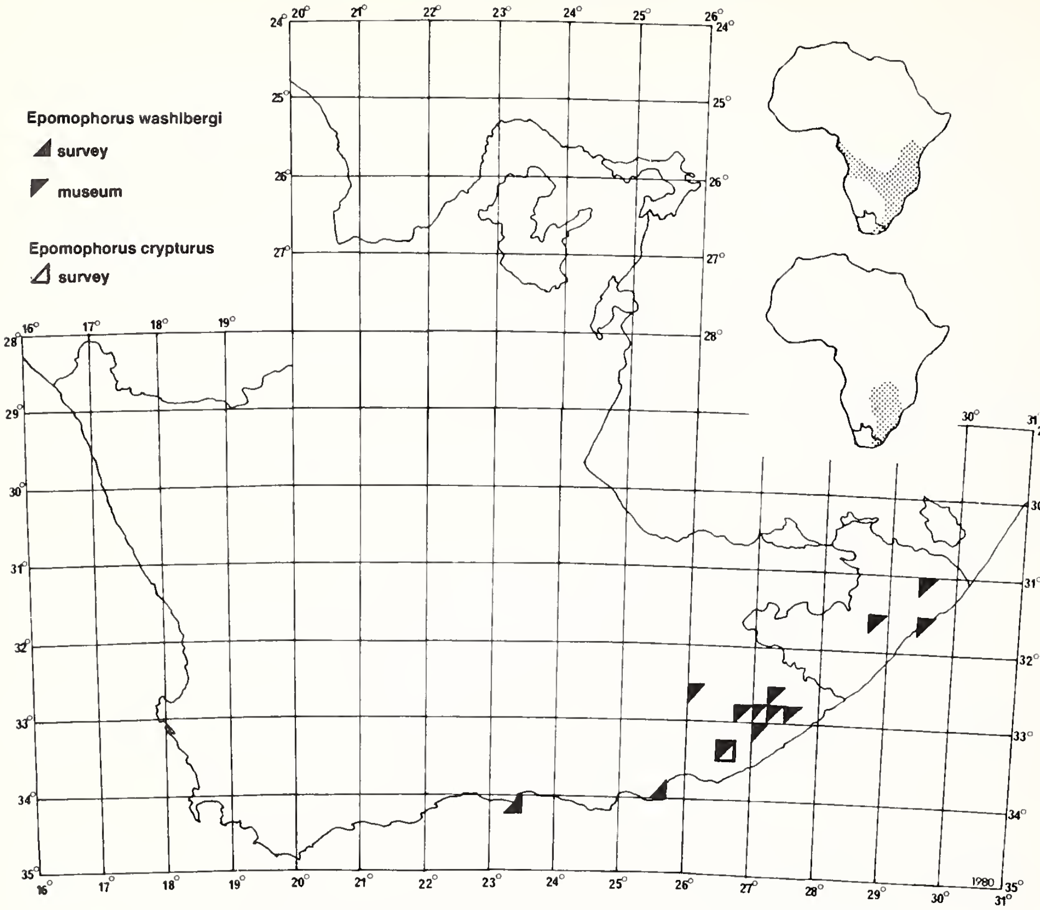

Fig. 3. The distribution of *Epomophorus wahlbergi* and *E. crypturus* in the Cape Province.

showed that the ranges overlap. The single specimen of *E. crypturus* collected had a forearm of 77,8 mm, which is just within the range of 77,5–85,5 mm the authors established for *E. wahlbergi*.

Distribution and status

According to Hayman & Hill (1971) this species occurs from the equator southwards across most of the continent, except for the dry western parts of South West Africa, the western Cape Province and the Karoo. Meester *et al.* (1964) state that it occurs in the eastern Cape, and Ellerman *et al.* (1953) record that it has been collected from Pirie.

During the survey one specimen was collected in Grahamstown, but no Cape specimens could be traced in the museums. The distribution in the Cape Province must therefore be very limited (Fig. 3), and the status of the species rare.

Material examined

Survey — 1 Grahamstown.

Eidolon helvum (Kerr, 1792) Straw-coloured Fruit Bat

This species is distinguished by its long wings, which are the longest for any bat in the Cape Province. They are also longer in proportion to the body than for any other bat in the area.

Distribution and status

This species occurs as a migrant over the entire continent, but is rarely recorded in southern Africa (Meester *et al.* 1964). A specimen from the Barkly West High School was shot in an orchard during 1976. Photographs of one shot in Middelburg (Cape) during 1970 were also examined.

Museum specimens are from localities as widely separated as Hondeklipbaai in the north-west Cape and Tylden in the eastern Cape. Other published localities include Bedford and Steynsburg (eastern Cape) and Griqualand West (Roberts 1951). Thus *E. helvum* may be found in most of the Cape Province, except for the southern and eastern coastal regions (Fig. 4). However, it is rare in this area and only visits during the summer fruiting season.

Habits

Little is recorded of the habits of *E. helvum* in the Cape Province. Where it occurs it is almost always found feeding in deciduous fruit trees.

Material examined

Survey — 1 Barkly West.

Museums — 1 Mazelsfontein (TM); 1 Hondeklipbaai, 1 Namaqualand, 1 Tylden, 1 Vryburg (SAM).

Rousettus aegyptiacus (E. Geoffroy, 1810) Egyptian Fruit Bat

This is the only cave-dwelling fruit bat species in the Cape Province. Hayman & Hill (1971) record that the Egyptian fruit bats occurring in the Cape Province belong to the subspecies *R. a. leachii*, although Roberts (1951) regarded *R. leachii* as a valid species.

Distribution and status

The Egyptian fruit bat occurs over a large part of Africa, but in the Cape Province it is restricted to the south-western, southern and eastern coastal regions (Fig. 4). Roberts (1951) states that it is rarely found inland from the coastal belt. It is therefore of interest that it was found in the Swartberg near Oudtshoorn and in the Winterhoek mountains near Porterville.

Some evidence of migration was found, although the distances involved were not very great. Bats that had been marked by G. R. Robinson at Storms River Mouth were collected during the fruit season of November to February in the Langkloof, about 50 km away. The species is abundant in its distribution area and gathers in large groups of up to a thousand in suitable caves.

Habits

These are the only fruit bats that are able to use echo-location, and this allows them to roost in dark caves. They were found in larger caves along the coastal areas, usually in associ-

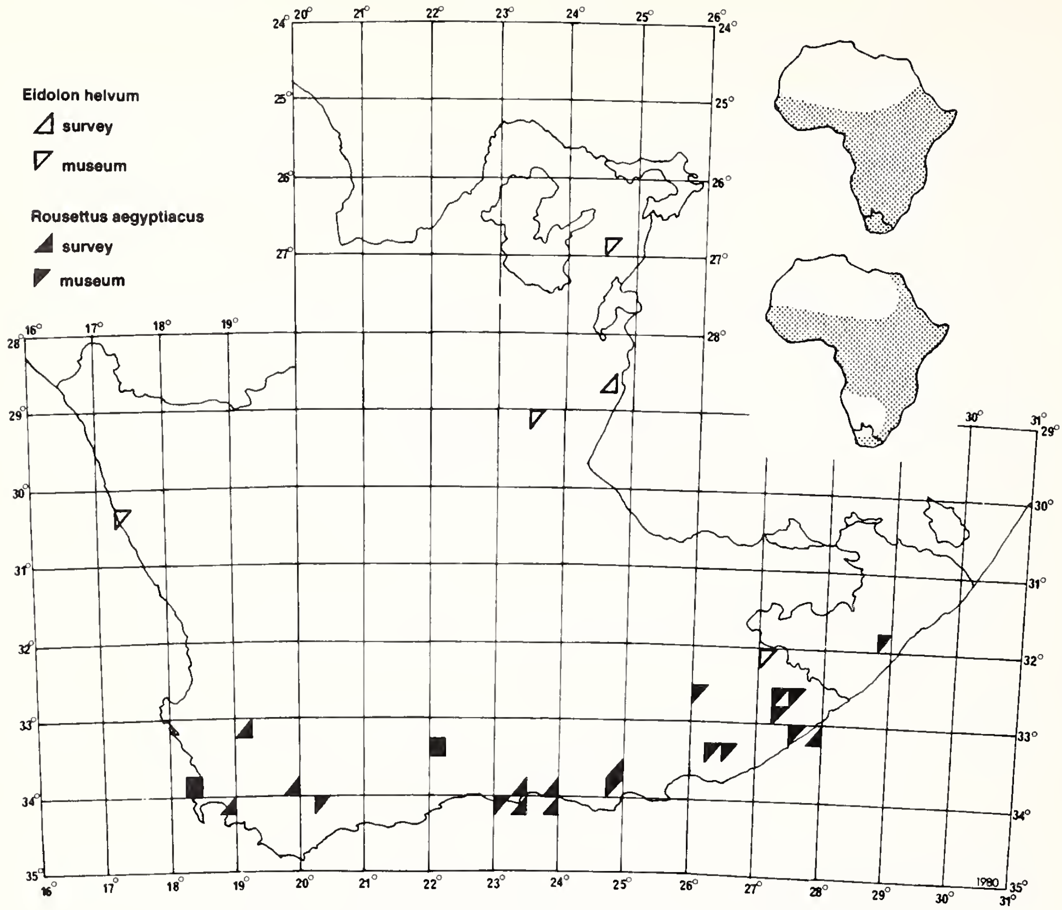

Fig. 4. The distribution of *Eidolon helvum* and *Rousettus aegyptiacus* in the Cape Province.

ation with up to four insectivorous species. They typically occupy the "twilight" areas just inside the entrances of caves, whereas the insectivorous species roost further in where it is completely dark. They are very noisy, and are easily alerted when the caves are entered.

Food

They were seen eating peaches, apricots, apples, loquats and the fruit of yellow-wood (*Podocarpus*) and hard pear (*Olinia*) trees. It appears that only ripe fruits are eaten, which means that damage in gardens and orchards only occurs during a short period. Thus the extent of damage caused is often exaggerated. For the greater part of the year they feed on wild fruit, and in this way act as important seed propagators of a wide range of indigenous plants and trees.

Breeding

Infants were seen at Helderberg Cave in early January, and some of the females caught then were still pregnant. During January 1978 females netted in a peach orchard near to this cave were carrying infants of about two-thirds their weight.

Material examined

Survey — 1 Bat's Cave, 3 Bean-se-bos, 1 Die Hel, 1 Helderberg, 2 Keurbooms Reserve, 1 Krakeel River, 1 Robertson, 3 Skeleton Cave, 1 Storms River Mouth, 1 Twee Riviere, 2 Wynberg.

Museums — 7 Knysna, 5 Skeleton Cave (TM); 1 Amabele, 1 East London, 2 King William's Town, 2 Patensie, 2 Pirie (KWT); 1 Knysna, 1 Table Mountain (SAM); 1 Amabele, 3 Bedford, 2 Grahamstown, 1 King William's Town, 2 Mqanduli, 1 Salem, 1 Swellendam (AM).

Suborder MICROCHIROPTERA: Family EMBALLONURIDAE

Taphozous mauritianus E. Geoffroy, 1818 — Mauritian Tomb Bat

This is the only species of the family occurring in the Cape Province. It can be recognized easily because its tail separates from the interfemoral membrane and merges on the upper side about half-way down its length.

Distribution and status

According to Hayman & Hill (1971) this species is widely distributed over a large part of the continent, in most savanna regions south of the Sahara. Meester *et al.* (1964) stated that its Cape distribution is limited to the southern and eastern Cape. No specimens were collected during the survey, but the two Cape specimens in the museums confirmed this southern and eastern distribution (Fig. 5). A specimen recently collected at Hartswater (2724 DD) by Erasmus & Rautenbach (in press) suggests that the species may prove to be sparsely distributed over most of the Cape Province.

Habits

Erasmus & Rautenbach (in press) state that this species has the habit of roosting head downwards against the trunks of large trees or under the eaves of buildings.

Material examined

Museums—1 Heidelberg (SAM); 1 Alicedale (AM).

Family NYCTERIDAE

Nycteris hispida (Schreber, 1775) — Hairy Slit-faced Bat

References to the occurrence of this species in the Cape Province (Ellerman *et al.* 1953, Meester *et al.* 1964) seem to be based entirely on a single dry skin housed in the South African Museum (ZM 5444) and prepared from a specimen that was collected at Port St Johns by Shortridge in 1902. It was caught at the same time as a series of more than 20 *N. thebaica* adults, but was separated from these on the grounds of its smaller size and lighter coat colour.

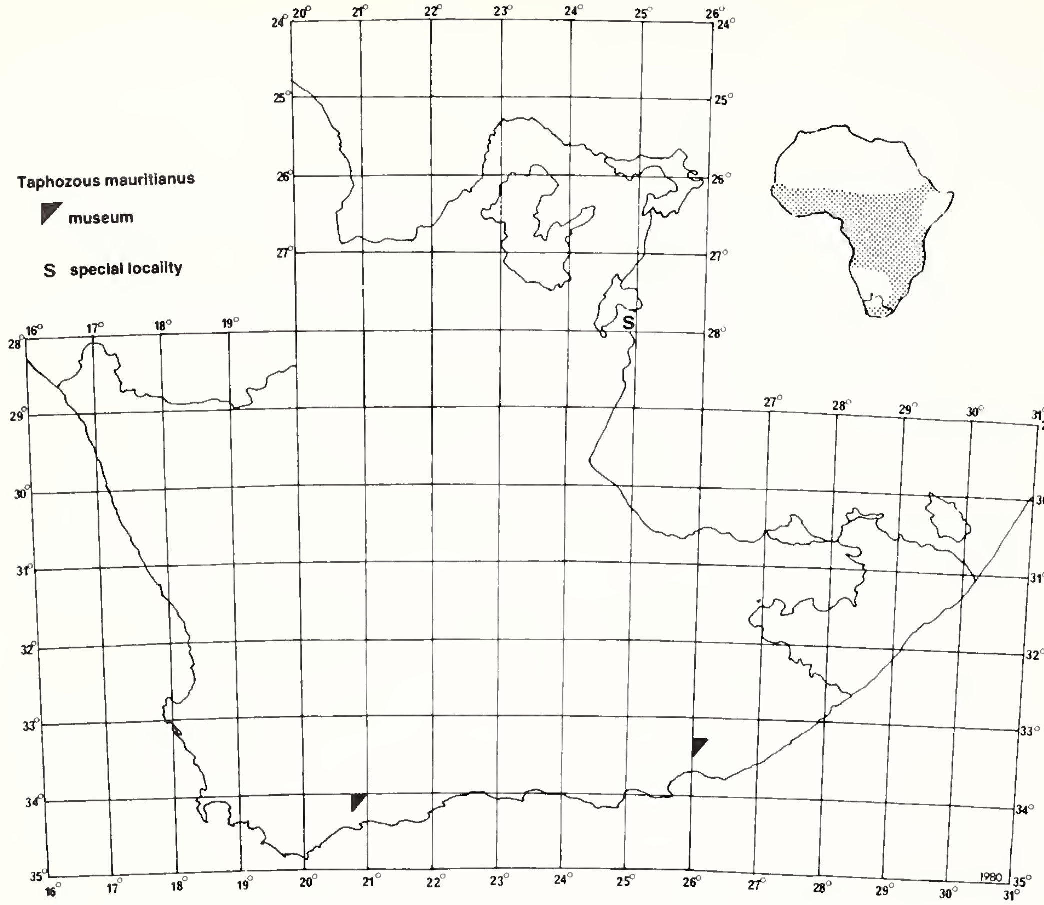

Fig. 5. The distribution of *Taphozous mauritianus* in the Cape Province.

However, it was caught in January, a time when one can expect to find juveniles of most bat species, and comparison with *N. thebaica* juveniles from other areas yields no reason why this specimen should be separated from the more common species. In the absence of further evidence the authors do not consider *N. hispida* as part of the Cape bat fauna.

Nycteris thebaica E. Geoffroy, 1818 — Egyptian Slit-faced Bat

This is the only species of the family Nycteridae that definitely occurs in the Cape Province. It is easily recognized by its very large oval ears. Another outstanding character is the deep groove, between the nose-leaves, which extends from the nostril to a line between the base of the ears.

Roberts (1951) regarded *N. capensis* as the senior synonym of *N. thebaica*, which he incorrectly attributed to A. Smith, 1834, and gave the subspecies *capensis* and *damarensis*. However, Ellerman *et al.* (1953) and Meester *et al.* (1964) recognized Geoffroy's earlier description

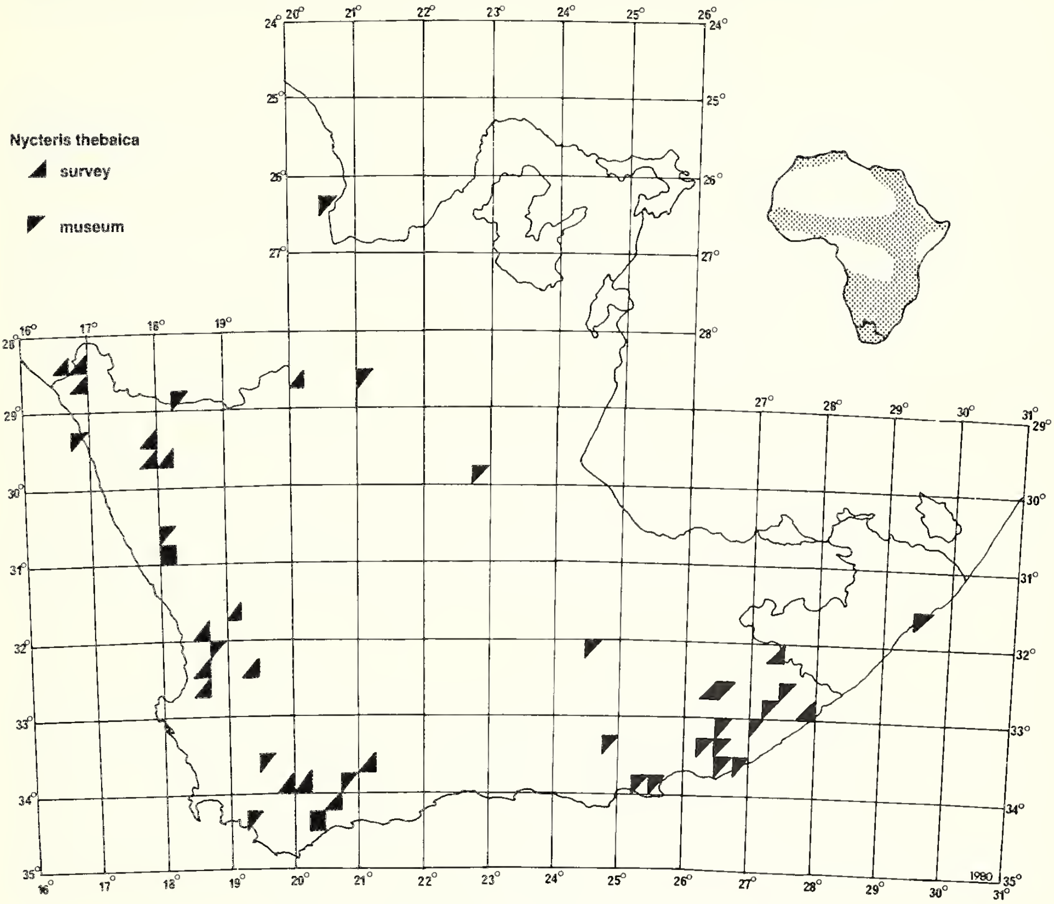

Fig. 6. The distribution of *Nycteris thebaica* in the Cape Province.

of *N. thebaica*, but listed the same subspecies. This was followed by Hayman & Hill (1971), although they did not commit themselves on the validity of the subspecies.

Distribution and status

N. thebaica is widely distributed in open country over most of Africa (Hayman & Hill 1971). In the Cape Province it occurs throughout the western, south-western and eastern parts of the province, although it has not been found in the forests of the southern coastal belt (Fig. 6). In spite of its wide distribution it is nowhere common.

Habits

These bats normally use caves, disused mines, undisturbed rooms and cellars as resting places, where they hang free from the roofs by their hind legs. They seem to prefer smaller caves or mines, where they gather in small numbers (up to 200 individuals of both sexes). They

were nearly always found on their own or with *Rhinolophus* species in the resting places, but in the De Hoop Cave they occurred with *Myotis tricolor* and *Miniopterus schreibersii*.

Slit-faced bats have characteristically long ears, suggesting that their hearing, and therefore echo-location ability, is very well-developed. This, combined with their manoeuvrability, meant that they were very difficult to catch in traps or mist-nets. This ability to manoeuvre around obstructions may explain why they were usually found deeper in the caves or mines than any other bat species. They normally fly low, about one metre above the ground, with a slow erratic flight pattern.

Some evidence of migration was found. In Namaqualand several caves were deserted for long periods in late summer and winter, and in the Bredasdorp area the slit-faced bats disappeared from the De Hoop Cave and Spitskop Mine for several months at a time. Too few bats were marked to allow the establishment of a pattern of migration, but it is unlikely that they migrate over very long distances.

Food

N. thebaica usually forages on or near the ground where it picks up ground insects and then carries them to suitable resting places before eating them. During the survey several such resting places were found. Some were adjacent to, or even in, the roosts. Food remains found in resting places in the Namaqualand and Richtersveld of the north-western Cape showed large numbers of bladder grasshoppers (Pneumoridae), and some scorpions and ordinary grasshoppers (Acrididae).

Breeding

Two females, each with a single infant, were taken at Forest Ranch during November and young infants were seen in the De Hoop Cave in December. Three females from Driefontein were caught in early November. All were pregnant with a single implanted foetus. A female collected in October from Sandberg was also pregnant whereas females collected during January and February were not pregnant. These data indicate that parturition occurs in November and December only, which is a markedly shorter period than the September—February period given by Smithers (1971) for the species in Botswana.

Material examined

Survey — 1 Amalinda, 1 Bakleisdrif, 1 Blouputs, 2 Brandkaros, 1 De Hoop, 1 Doringkraal, 2 Doringpoort River, 4 Driefontein, 2 Forest Ranch, 3 Hester Malan, 6 Kersbos, 1 Kroomie, 1 McGregor, 1 Montagu Cave, 3 Okiep, 1 Sandberg, 1 Sewefontein, 1 Skrik van Rondom, 1 Spitskop, 5 Vrolijkheid, 2 Welbedacht Mine, 1 Wondergat.

Museums — 1 Goodhouse, 11 Grahamstown, 5 Grootvadersbos, 3 Keikamspoort, 11 Kersbos, 6 Twee Riviere (TM); 1 Alice, 2 Atherstone, 3 Compagnies Drift, 1 Garies, 5 Goodhouse, 1 Graaff-Reinet, 14 Rangerton (KWT); 1 De Hoop, 1 Hawston, 1 Hex River, 21 Port St Johns (SAM); 1 Abbotsburg, 7 Brakkloof, 2 Despatch, 1 Fort Brown, 1 Glenlea, 4 Grahamstown, 6 Kleinpoort, 1 Lessendrum, 1 Manley Flats, 1 Moneysworth, 1 Port Alfred, 1 Port Elizabeth, 1 Salem, 1 Stones Hill (AM).

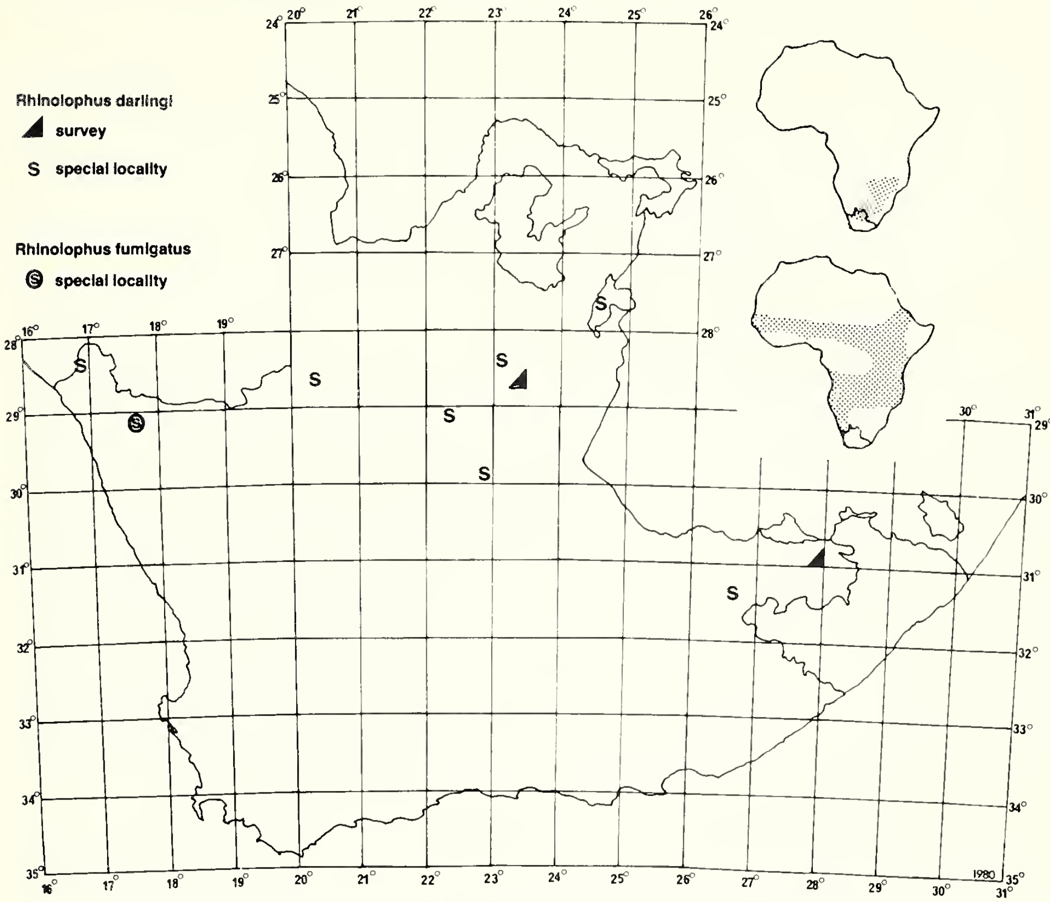

Fig. 7. The distribution of *Rhinolophus darlingi* and *Rhinolophus fumigatus* in the Cape Province.

Family RHINOLOPHIDAE

Bats of this family have a distinct horseshoe-shaped nose-leaf with a pointed lancet behind the horseshoe. Species distinction rests mainly on the form of this structure, with dentition and forearm length as secondary characteristics. However, as the taxonomy of several of the species occurring in the Cape Province is rather confused the whole genus probably needs revision.

Rhinolophus fumigatus Rüppell, 1842 — Rüppell's Horseshoe Bat

There is some argument whether *R. fumigatus* should include the subspecies *aethiops* or whether *aethiops* should be a species in its own right (Hayman & Hill 1971). Either way this large *Rhinolophus* appears to be very rare in the Cape Province if it occurs at all. All mention

of its occurrence (Shortridge 1942, Roberts 1951, Ellerman *et al.* 1953, Hayman & Hill 1971) seems to be based on two specimens collected in 1903 by C. H. B. Grant at Klipfontein, Little Namaqualand (Fig. 7). These are housed in the British Museum of Natural History (J. E. Hill pers. comm.).

A *Rhinolophus* specimen, in the Transvaal Museum, collected by Roberts at Soetendalsvlei in the south-western Cape and labelled as *R. fumigatus*, appears to be *R. clivosus*. This identification is supported by Rautenbach (pers. comm.).

No specimens were collected during the survey and there are no specimens from the Cape Province in the South African museums.

Rhinolophus darlingi K. Andersen, 1905 — Darling's Horseshoe Bat

Until recently this bat had not been recorded from the Cape Province. During the survey all of the medium-sized *Rhinolophus* were identified as either *R. clivosus* or *R. capensis*. However, a recent reassessment by Erasmus & Rautenbach (in press) of several specimens collected in the Cape Province, including four bats collected during the survey, suggests that *R. darlingi* may also be present. These authors used one external and fifteen cranial measurements for a computerized multivariate analysis and chromosome karyotyping. The results are still somewhat confusing, since clear diagnostic characters did not emerge. Erasmus & Rautenbach were able to differentiate between *R. clivosus* and the other two species using some of the measurements and also chromosome structure. However, they were unable to separate *R.capensis* and *R. darlingi* with ease since the analysis did not attach much significance to the position of the small premolar. This was used as a diagnostic character by Hayman & Hill (1971) and for the present study. Erasmus & Rautenbach (in press) separated *R. darlingi* from *R. capensis* mostly on allopatry. There is a clear need for further work on the medium-sized *Rhinolophus* group and this is at present being undertaken by Rautenbach (pers. comm.).

Distribution and status

The localities listed for *R. darlingi* by Erasmus & Rautenbach (in press) as well as the four survey specimens identified as this species are shown in Fig. 7. These suggest that the species is widely distributed in the northern Cape. The most westerly locality in the Richtersveld (2816 BD) is in the same locus as a series of *R. capensis* caught during the survey (Fig. 9), which throws some doubt on the complete allopatric separation of the two species.

Because of the taxonomic confusion a statement regarding the species' conservation status cannot be made, although Erasmus & Rautenbach (in press) suggest that it may be fairly common and widespread wherever suitable roosts such as deep caves or old mines are available.

Material examined

Survey — 3 Glass Nevie, 1 Koegelbeen Cave.

Rhinolophus clivosus Cretzschmar, 1826 — Geoffroy's Horseshoe Bat

In this species the anterior upper premolar is either absent or lies outside the tooth row, so that the canine and second premolar are in contact (Hayman & Hill 1971). The forearms of 133 specimens caught during the survey range in length from 51,3 mm to 57,8 mm.

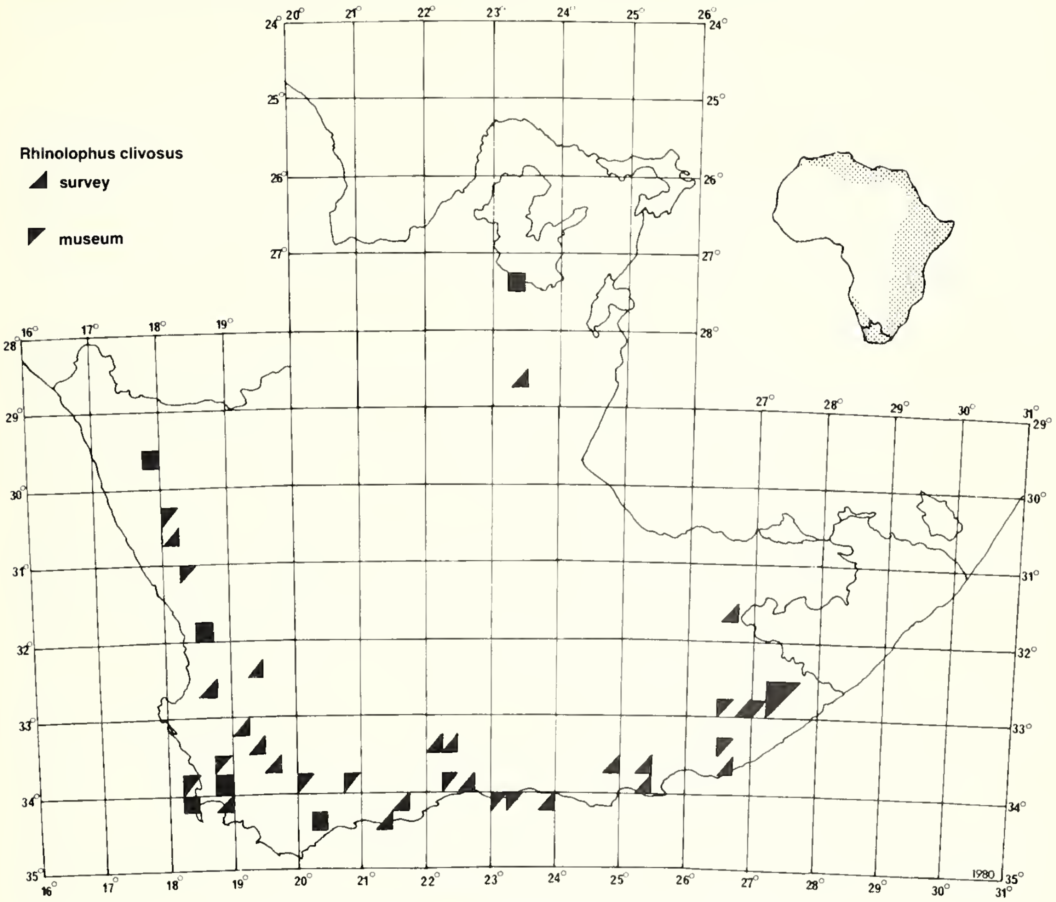

Fig. 8. The distribution of *Rhinolophus clivosus* in the Cape Province.

Distribution and status

According to Hayman & Hill (1971) *R. clivosus* occurs over much of the African continent except for the West African and the Congo forest belt. In the Cape Province it is abundant throughout the western, southern and eastern parts, but not the central Karoo (Fig. 8). Specimens were collected wherever suitable caves or disused mines were found. Although colonies of up to ten thousand exist in caves such as De Hoop and Koegelbeen, numbers appear to have declined in other roosts due to human disturbance.

Habits

This is a typical cave-bat, and the great majority of specimens were taken from caves or disused mines. However, on two occasions specimens were collected from cellars beneath

houses. Elsewhere (Herselman & Norton in prep.) evidence is presented of short-distance migration of up to 10 km in the south-western Cape.

They are low altitude fliers and often hunt below treetop level between the shrubs, where they catch low-flying insects.

Breeding

In population studies carried out at the De Hoop Cave it was found that the infants are born from the middle of December onwards (Herselman unpublished data). Single-foetus implantation is the rule. Fertility is high, 92% of a sample of 150 females caught in November having been pregnant.

Material examined

Survey — 1 Alice Mission, 5 Apies River Forestry Station, 4 Bean-se-bos, 1 Boomslang Cave, 1 Cango Caves, 51 De Hoop, 1 Dennebos, 2 Die Oog, 8 Die Hel, 2 Driefontein, 2 Droëvlakte, 3 Glass Nevie, 1 Gordon's Bay, 1 Grahamstown, 1 Jonkershoek, 2 Klipfontein, 5 Koegelbeen Cave, 3 Koo Cave, 13 Maitland Mines, 5 Roodebergskloof, 2 Sandile's Cave, 1 Simon van der Stel Mine, 4 Skeleton Cave, 2 Skrik van Rondom, 1 Skurweberg Cave, 2 Spitskop, 2 Sterkstroom, 1 Storms River Mouth.

Museums — 2 Berg River, 3 Grootvadersbos, 1 Hester Malan, 3 Klawer, 5 Knysna, 1 Lourens Farm (TM); 2 Ezelfontein, 1 Fort Beaufort, 1 Kei Road, 11 King William's Town, 21 Kuruman, 3 Pirie (KWT); 1 Boomslang Cave, 1 Camps Bay, 1 De Hoop, 1 Plettenbergbaai, 1 Stellenbosch (SAM); 5 Fort Beaufort, 1 George, 3 Gleniffer, 1 Grahamstown, 2 Pirie (AM).

Rhinolophus capensis Lichtenstein, 1823 — Cape Horseshoe Bat

This species is very similar in colour and general appearance to *R. clivosus*. Species distinction is based on dentition. *R. capensis* has the small anterior upper premolar lying within the tooth row, so that the canine and second premolar are not in contact, whereas in *R. clivosus* this tooth is either absent or lies outside the tooth row. However, in some individuals it was difficult to say with certainty whether the tooth was within or outside the tooth row and this, combined with the fact that the two species were usually found together, made them difficult to separate. The forearm lengths of 50–57 mm for *R. clivosus* and 47–51 mm for *R. capensis* given in Hayman & Hill (1971) could not be used as a character, since in the present study a greater overlap of 51–58 mm and 46–53 mm respectively was found.

Distribution and status

Although Hayman & Hill (1971) record that *R. capensis* occurs from Zambia southwards through Natal to the Cape Province, recent re-examination of the material suggests that all the specimens from outside the Cape Province are actually *R. darlingi* (Smithers 1983). This means that *R. capensis* is probably endemic to the province.

During the survey roosts were found all along the coastal areas of the southern and eastern Cape but none in Namaqualand, an area where specimens had previously been collected from several localities (Fig. 9).

Within its restricted range in the southern parts of the Cape Province *R. capensis* appears to be fairly common, several cave systems having colonies of more than a thousand individuals.

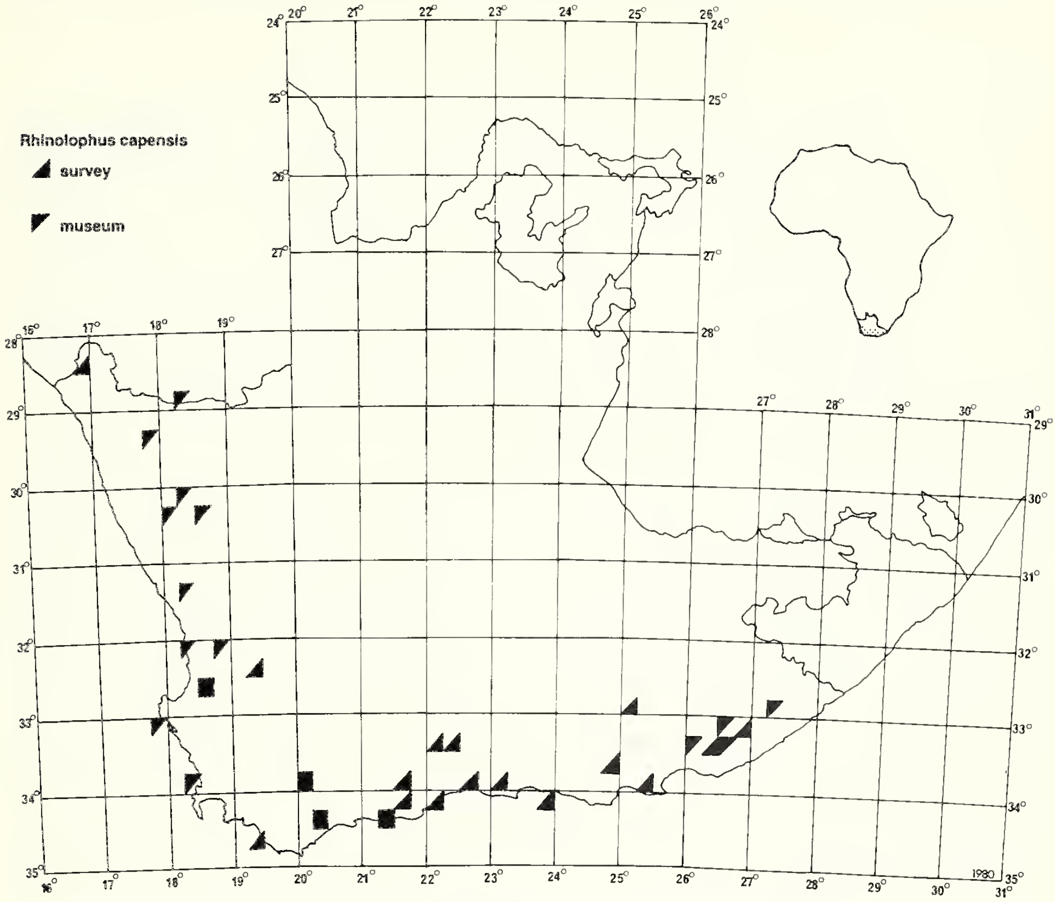

Fig. 9. The distribution of *Rhinolophus capensis* in the Cape Province.

Habits

All the survey specimens were found roosting in caves or disused mines, both sexes being found together. In the south-western Cape the species migrates short distances of up to 10 km (Herselman & Norton in prep.). It shows a typically erratic flight-pattern at low altitudes, and feeds mainly on low-flying insects.

R. capensis was often found in the same situations as *R. clivosus*, although clusters of the two species seemed to keep separate. Because of their similarity in size, shape and distribution it is not clear how they differ ecologically, and this is a subject that deserves further study.

Breeding

At the De Hoop Cave it was found that a single infant is born from the middle of December onwards. Infants are carried by their mothers during the day, but are left behind when the

adults are feeding. Samples taken from De Hoop in November showed a fertility of 86% among the females.

Material examined

Survey — 3 Abrie, 1 Bean-se-bos, 10 Bloukrans, 3 Breakfast Vlei, 66 De Hoop, 1 Dennebos, 1 Die Kelders, 10 Droëvlakte, 7 Grootplaas Cave, 6 Keurbosfontein, 4 Klipfontein, 3 Maitland Mines, 5 Marcus Mud Crawl, 6 Millwood Mines, 2 Montagu Cave, 1 Salem, 7 Skrik van Rondom, 6 Spies Cave, 2 Spitskop, 2 Storms River Mouth, 5 Tunnel Cave, 6 Wondergat.

Museums — 4 Klawer, 1 Kleinpoort, 3 Saldanha Bay, 1 Stilbaai (TM); 4 Compagnies Drift, 2 Ezelfontein, 2 Goodhouse, 20 Het Kruis, 10 King William's Town, 35 Orrelgat, 1 Paddagat (KWT); 2 Cape Town, 1 Clanwilliam, 2 De Hoop, 14 Montagu (SAM); 1 Alicedale, 1 Brakkloof, 1 Grahamstown, 1 Het Kruis, 2 Orrelgat, 10 Slaaikraal (AM).

Rhinolophus denti Thomas, 1904 — Dent's Horseshoe Bat

This small *Rhinolophus* is very similar in appearance to *R. swinnyi* and it is possible that they are conspecific. Neither species has been collected in the Cape Province in the last half century.

No specimens of *R. denti* could be traced in the South African museums, although there are two specimens in the British Museum of Natural History from Louisvale near Upington and Kuruman (J. E. Hill pers. comm.); (Fig. 10).

Whether *R. denti* is included with *R. swinnyi* or not the species can be considered as extremely rare, possibly even extinct, in the Cape Province.

Rhinolophus swinnyi Gough, 1908 — Swinny's Horseshoe Bat

R. swinnyi is the smallest species in the genus, with a forearm length of about 42,5–43,8 mm, (Roberts 1951).

Distribution and status

Hayman & Hill (1971) state that *R. swinnyi* occurs in the eastern Cape Province and extends northwards to Tanzania. However, it appears to be very rare in the Cape Province. During the survey no specimens were collected and only 20 museum specimens, all collected before 1940, were examined (Fig. 10). All these specimens were from only two grid squares, which suggests that *R. swinnyi* was only marginally distributed in the Cape Province. The lack of recent material indicates that it may no longer occur in the province.

Material examined

Museums — 3 King William's Town, 4 Pirie, 1 Ross Mission (KWT); 5 Pirie (SAM); 7 Pirie (AM).

Hipposideros caffer (Sundevall, 1846) — African Leaf-nosed Bat

Before the survey two subspecies had been recorded from southern Africa, *H. c. caffer* in the eastern Cape and northwards up the east coast, and *H. c. angolensis* in northern South West Africa (Hayman & Hill 1971). A series of 21 specimens of *H. c. caffer* from Port St Johns

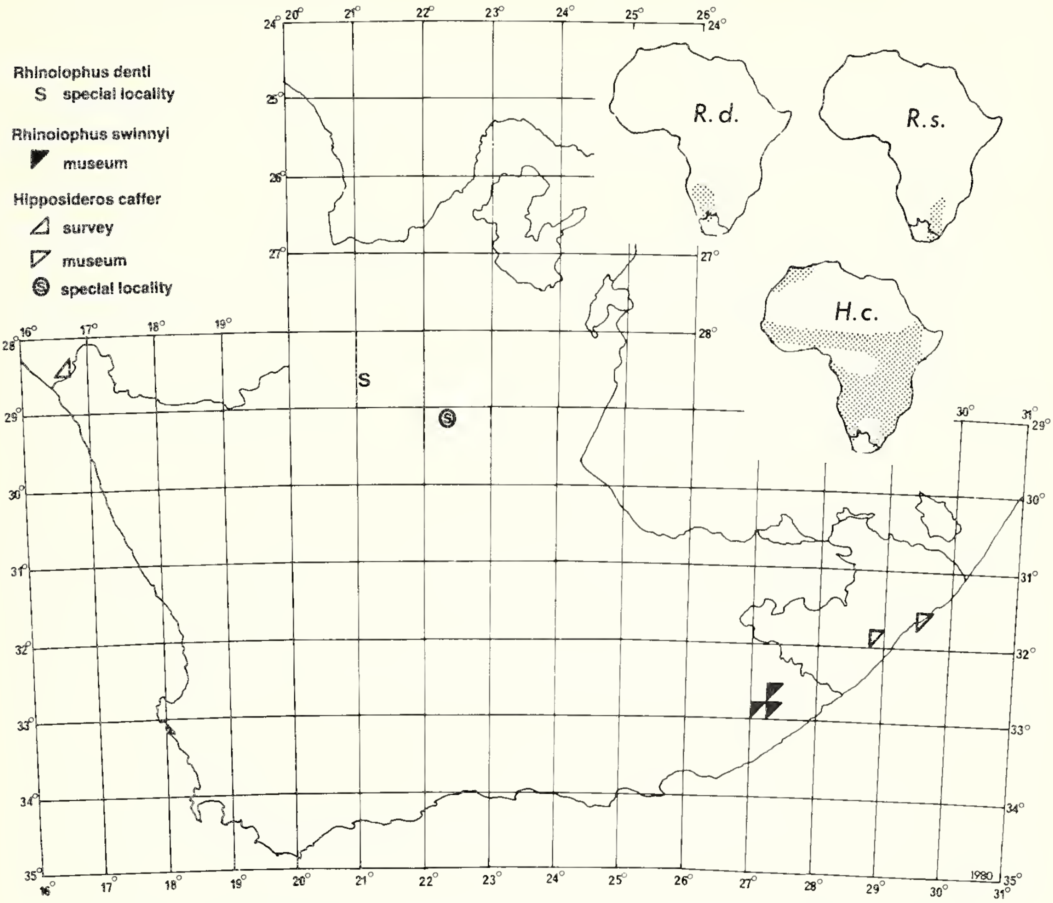

Fig. 10. The distribution of *Rhinolophus denti, R. swinnyi* and *Hipposideros caffer* in the Cape Province.

in the S.A. Museum was examined. The average forearm length of these specimens is 48,2 mm, which led Roberts (1951) to state that this subspecies is smaller than *H. c. angolensis*, which has a forearm measuring 50,3 mm. However, the authors collected two specimens with a mean forearm length of 47,4 mm at Brandkaros in the Richtersveld. This measurement tends to identify these specimens as *H. c. caffer*, but their occurrence in the northern Cape suggests that they should be *H. c. angolensis*. Therefore criteria other than forearm length should be found for subspecific division of this species.

Distribution and status

Mentions of the presence of this species in the Cape Province prior to the survey (e.g. Roberts 1951, Hayman & Hill 1971) appear to have been based on very old (before 1930) specimens from Port St Johns and Mqanduli in Transkei (Fig. 10). It has not been collected

since and this, together with the excision of Transkei, means that the subspecies *H. c. caffer* is unlikely to occur within the present borders of the Cape Province. The two specimens from the Richtersveld, collected during the survey (Fig. 10), showed that the Angolan subspecies *H. c. angolensis* occurs in the north-western Cape and three specimens collected recently by Erasmus & Rautenbach (in press) near Marydale (2922AB) suggest that it may be even more widely distributed. Hayman & Hill (1971) record that it is widespread in the drier woodland and savanna regions of Africa.

Habits

The two specimens were found roosting in a small cave with a very narrow entrance, which they shared with individuals of *Nycteris thebaica*. Erasmus & Rautenbach (in press) found three *H. caffer* roosting in an old mine.

Material examined

Survey — 2 Brandkaros.

Museums — 21 Port St Johns (SAM); 3 Mqanduli (AM).

Family VESPERTILIONIDAE

This is a very large family, several species of which are widespread in the Cape Province. They are strong fliers and many species look very similar in appearance. Since external features are often insufficiently marked to make generic identification certain, Hayman & Hill (1971) found it necessary to use dental formulae and tooth patterns in their key to the genera. These, together with ear length, forearm length and a few other characteristics, form the basis of species distinction.

Myotis seabrai (Thomas, 1912) Angola Wing-gland Bat

Bats of the genus *Myotis* have 38 teeth, which is more than that in all other genera in the family except *Kerivoula*. However, the latter is easily distinguished by its highly-elevated cranium.

Whereas Roberts (1951) treated both *Myotis* and *Cistugo* as full genera, Ellerman *et al.* (1953) and Hayman & Hill (1971) recognized *Myotis* as the genus with two subgenera, *Selysius* and *Cistugo*. *M. tricolor* was then placed in the subgenus *Selysius* and *M. lesueuri* and *M. seabrai* in the subgenus *Cistugo*.

Bats of the subgenus *Cistugo* are among the rarest in the world and therefore deserve special attention. They are the only bats on the continent that possess wing-glands. The subgenus has been divided into two species on the basis of forearm length and the position of the wing-glands. Both of these characters show some variation and therefore more taxonomic work will have to be done to separate them convincingly.

The wing-glands of *M. seabrai* are recorded as being larger than in *M. lesueuri* and lie in various positions on the wing, whereas those of *M. lesueuri* are always found close to the forearm (Shortridge 1942). Shortridge also records that in several instances there are two glands together on either side, and the same was found in one of the survey specimens. *M. seabrai* is recorded as being smaller in size than *M. lesueuri*. The five survey specimens have forearm lengths between 30,2 mm and 33,2 mm, with a mean of 31,9 mm.

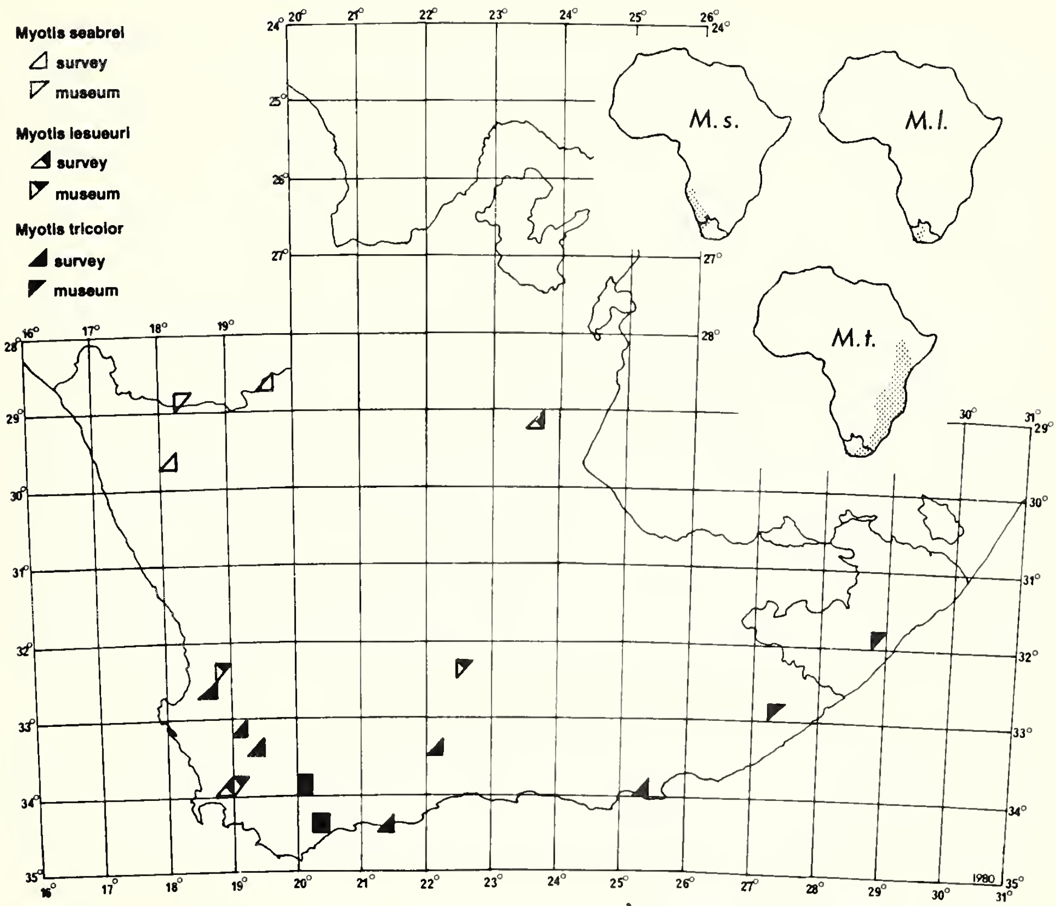

Fig. 11. The distribution of *Myotis seabrai, M. lesueuri* and *M. tricolor* in the Cape Province.

Distribution and status

M. seabrai has a very limited distribution in the Cape Province, occurring only in the north-western parts (Fig. 11). From there it extends northwards through South West Africa to Angola. It had previously been collected only from Goodhouse which suggests that it is rare in the Cape. However, Shortridge (1942) stated that it was the most plentiful bat around Goodhouse Citrus Estate. A similar situation was found at Steyerskraal, 100 km east of Goodhouse, where three specimens from a large number of bats flying next to a river were shot. Two specimens were also netted over water at Goegab, 100 km south of Goodhouse. Further collecting may show this bat to be fairly common within a very restricted range in the Cape Province.

Habits

Because the survey specimens were either shot in flight or netted over water no information on their roosts was obtained. They were collected shortly after sundown while flying a few metres above the ground. Roberts (1951) records this species flying low amongst orange trees and snapping small insects from the leaves.

Material examined

Survey — 2 Goegab, 3 Steyerskraal.

Museums — 8 Goodhouse (KWT).

Myotis lesueuri (Roberts, 1919) Lesueur's Wing-gland Bat

This species is very similar in size and colour to *Eptesicus*. However, the latter can easily be distinguished by its dentition, since it has two minute upper premolars lying transverse to the tooth row. There seems to be some confusion in the literature about the presence of wing-glands. Roberts (1951) states that no glands were visible in the dry skin of the wing of the type specimen, a male collected at Franschhoek in 1919. Similarly, the authors could find no wing-glands on two study skins from specimens collected at Citrusdal in 1937 by Shortridge and now housed in the Kaffrarian Museum. Further, Hayman & Hill (1971) question whether wing-glands are present or not. The answer to the controversy may lie in Shortridge's (1942) suggestion that "in dry skins the glands become absorbed and lost to sight". During the survey a male taken from a trap in Jonkershoek in 1978 shows a small gland close to the forearm on the left wing only. A specimen collected in January 1979 near Beaufort West by staff of the Transvaal Museum also has a small gland on the right wing close to the forearm.

Distribution and status

In total only eight specimens of this bat have been collected in the Cape. The survey shows that the distribution is not as restricted to the south-western Cape as was previously thought (Fig. 11). The specimens collected in the Great Karoo and in the northern Cape suggest that it may occur in most of the Cape Province. However, there is no doubt that it is very scarce and therefore deserves special attention. If it is a valid species separate from *M. seabrai* it is probably endemic to the province.

Material examined

Survey — 1 Jonkershoek, 1 Mazelsfontein.

Museums — 2 Hex River Estate (KWT); 1 Beaufort West, 1 Saasveld (TM).

Myotis tricolor (Temminck, 1832) Cape Hairy Bat

Distribution and status

M. tricolor occurs in the southern part of the Cape Province, from Citrusdal in the south-west to King William's Town in the east (Fig. 11). From there it is widely distributed up the eastern side of Africa as far as Ethiopia. It is not very abundant in the Cape Province and only a few museum records exist. During the survey 44 specimens were collected from nine localities.

Habits

One specimen from Michell's Pass was netted flying over water. The others were all found roosting in caves and mines. It appears that this species prefers larger caves that are relatively undisturbed, usually ones that contain pools of water. On every occasion the authors found it in the same roosts as *Miniopterus schreibersii* and it usually mixed freely with this species in daytime clusters on the walls. It has well-developed jaws and teeth and is difficult to handle. Other bats are sometimes bitten to death when they are placed together with this species in collecting bags.

Evidence of migration was found when a *Myotis tricolor* was recaptured in Montagu Cave, at a distance of 90 km from De Hoop Cave where it was banded. Kingdon (1974) states that all-male and all-female colonies have been found in various parts of the world, indicating that a certain amount of migration must take place. In New England Davis & Hitchcock (1965) found winter and summer migration of a related species *M. lucifugus* over distances of up to 275 km.

Breeding

Several juveniles were seen in Gant's Mine near Port Elizabeth during November 1976. Three pregnant females with single embryos and a female with a juvenile were taken in Montagu Cave towards the end of October 1979. At that time none of the other cave inhabitants, *Miniopterus schreibersii* and *Rhinolophus capensis*, had young. The same was found in the De Hoop Cave (Herselman unpublished data), where the *Myotis tricolor* gave birth from the end of October to the middle of November.

At night, when the adults emerge to feed, the juveniles are left in thickly-packed clusters against the walls of the cave or mine.

Material examined

Survey — 7 De Hoop, 4 Die Hel, 3 Droëvlakte, 12 Gant's Mine, 8 Marcus Mud Crawl, 1 Michell's Pass, 7 Montagu Cave, 1 Skrik van Rondom, 1 Skurweberg Cave.

Museums — 10 King William's Town (KWT); 2 De Hoop, 2 Montagu (SAM); 1 King William's Town, 1 Mqanduli (AM).

Pipistrellus nanus (Peters, 1852) Banana Bat

There are two members of the genus *Pipistrellus* recorded from the Cape Province, *P. nanus* and *P. kuhlii*, and both appear to be only marginally distributed in the eastern Cape. They are rather difficult to distinguish and during the survey nearly half of the specimens from the Cape Province in the South African museums were found to be incorrectly identified. It was found that the character of a "hatchet-shaped tragus" listed for *P. nanus* in Hayman & Hill (1971) was rather confusing. To differentiate these two species the present authors preferred to ignore this character and base identification on the second upper incisor, which is reduced in *P. kuhlii* and not in *P. nanus*, as well as on the more domed cranium of *P. nanus*.

As the popular name implies *P. nanus* is known to roost in banana trees. However, during the survey an intensive search in banana plants on several farms in the eastern Cape yielded no specimens. Their occurrence is therefore based on several rather old specimens from the Albany and South African Museums.

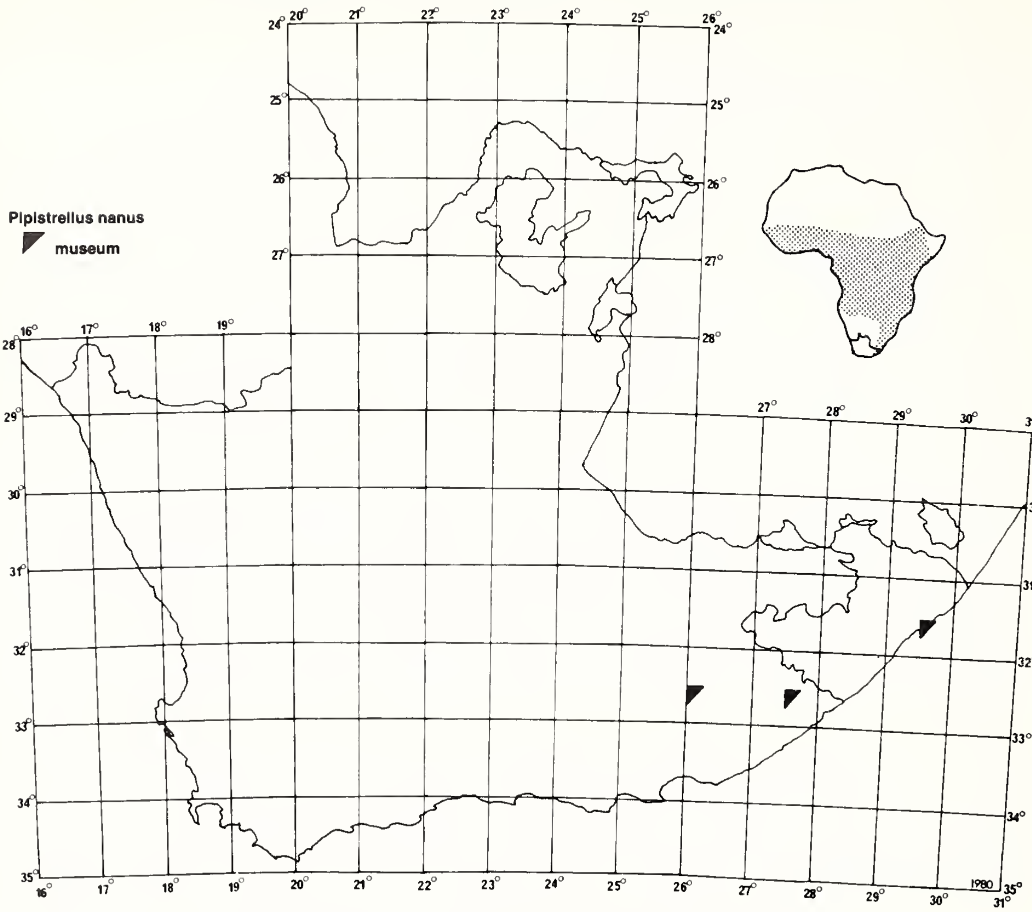

Fig. 12. The distribution of *Pipistrellus nanus* in the Cape Province.

Distribution and status

The banana bat has been recorded as widespread in the eastern Cape Province from as far south as East London (Ellerman *et al.* 1953). The museum records (Fig. 12) support their past occurrence there, although the lack of more recent material suggests that their range may have decreased from the south. A further factor is that a large part of the range mentioned by Ellerman *et al.* (1953) has been excised to form Transkei, and therefore its present range in the Cape Province is probably restricted. However, this tropical species is widespread up the east coast and in central Africa and lives in plantations of cultivated plants. Therefore its overall conservation status is probably secure.

Material examined

Museums—1 Bedford, 2 Port St Johns (SAM); 1 Kei Road (AM).

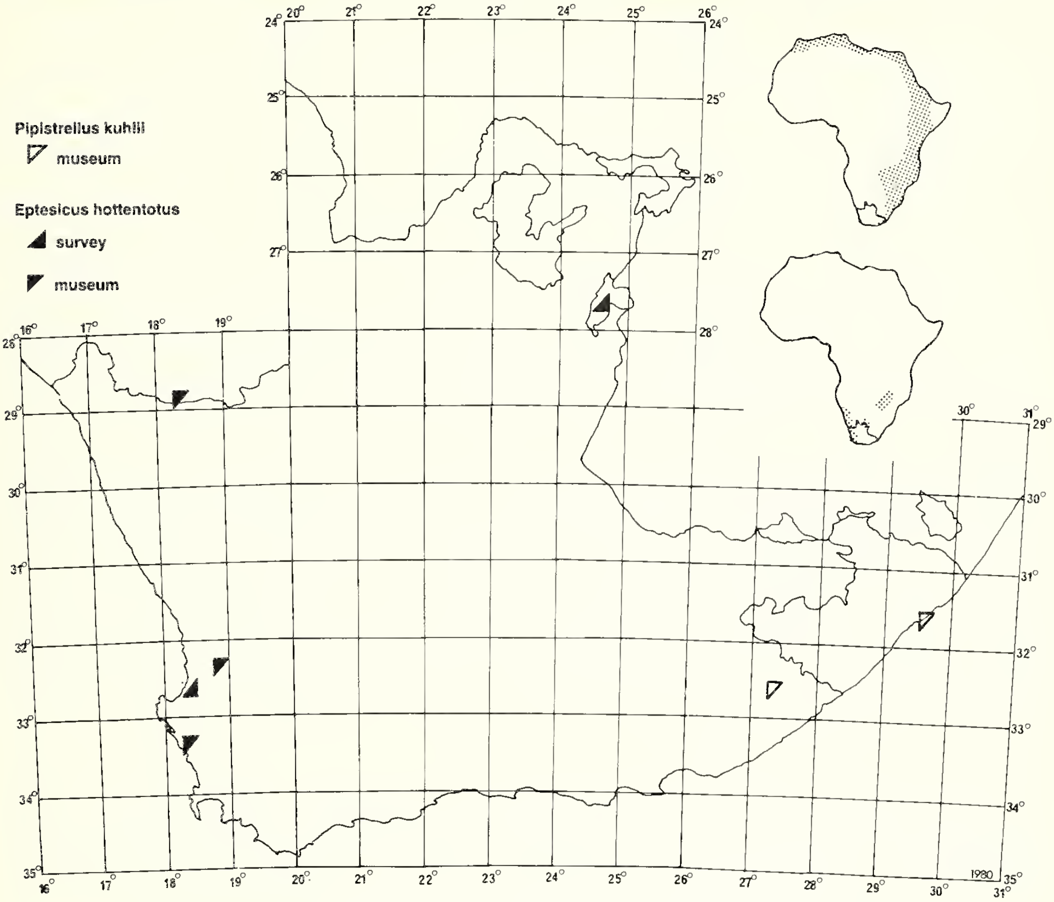

Fig. 13. The distribution of *Pipistrellus kuhlii* and *Eptesicus hottentotus* in the Cape Province.

Pipistrellus kuhlii (Natterer, 1817) Kuhl's Pipistrelle

Roberts (1951) separated the species *kuhlii* from the genus *Pipistrellus* and placed it in the genus *Romicia*. However, subsequent authors (Ellerman *et al.* 1953, Hayman & Hill 1971) do not recognize this separation.

Distribution and status

This marginal species appears to be very rare in the Cape Province, although it is widespread up the east coast of Africa and into Europe (Hayman & Hill 1971). Roberts (1951) and Ellerman *et al.* (1953) state that it occurs from the forested areas of the southern and eastern Cape as far west as Knysna. During the survey no material was collected and the only museum specimens which could be traced were from the eastern Cape and Transkei (Fig. 13).

Habits

Little is known of its habits, most specimens being caught when flying at night, either inside forests or not far from them (Roberts 1951). Smithers (1971) and Rautenbach (1982) found them roosting under the loose bark of dead trees.

Material examined

Museums — 1 Port St Johns (SAM); 2 Pirie (AM).

Eptesicus hottentotus (A. Smith, 1833) Long-tailed House Bat

This species is noticeably larger than any other *Eptesicus* in the Cape Province. Two subspecies, *E. h. hottentotus* and *E. h. pallidior*, are mentioned in checklists of mammals of South Africa. Roberts (1951) and Meester *et al.* (1964) list the distribution range of *E. h. hottentotus* as the eastern, southern and south-western Cape as far north as the mountains of Little Namaqualand, and that of *E. h. pallidior* as the north-western Cape Province and South West Africa.

According to Roberts (1951) *E. h. hottentotus* has a slightly shorter wingspan and a darker colour than *E. h. pallidior*, which is light yellow in colour. However, the specimens obtained during the study do not support such a clearcut division with respect to wing-length and colour. A female caught at Rocherpan on the west coast in April 1978 is dark in colour and has a forearm length of 47,5 mm, thus showing characteristics of *E. h. hottentotus*. Five specimens caught at Taung in Bophuthatswana, which falls within the distribution of *E. h. pallidior*, cannot be separated from the Rocherpan specimen. Their colour is also dark brown and their forearm lengths range from 47,0 to 51,5 mm, which is not noticeably greater than that of the Rocherpan specimen.

Distribution and status

The Taung series was collected about 400 km to the east of the South West African border and about 600 km east of Goodhouse, which was the most easterly site where *E. h. pallidior* had been collected before the survey. Therefore, it probably also occurs in the western Transvaal and southern Botswana although it has never been collected in these areas.

The new localities show a wide distribution of *E. h. pallidior* in the western, north-western and northern Cape Province (Fig. 13). However, the species is rare in the Cape Province, since only six specimens from two localities were collected during the survey. There are a further seven specimens in the South African museums. They are from three localities and were all collected before 1938.

Habits

The Rocherpan specimens were netted flying low over a marsh and the Taung series was taken from a small hollow in rocks situated at the entrance to an old mine tunnel inhabited by *Miniopterus schreibersii*.

Material examined

Survey — 1 Rocherpan, 5 Taung.

Museums — 4 Goodhouse, 2 Hex River Estate (KWT); 1 Cape Town (SAM).

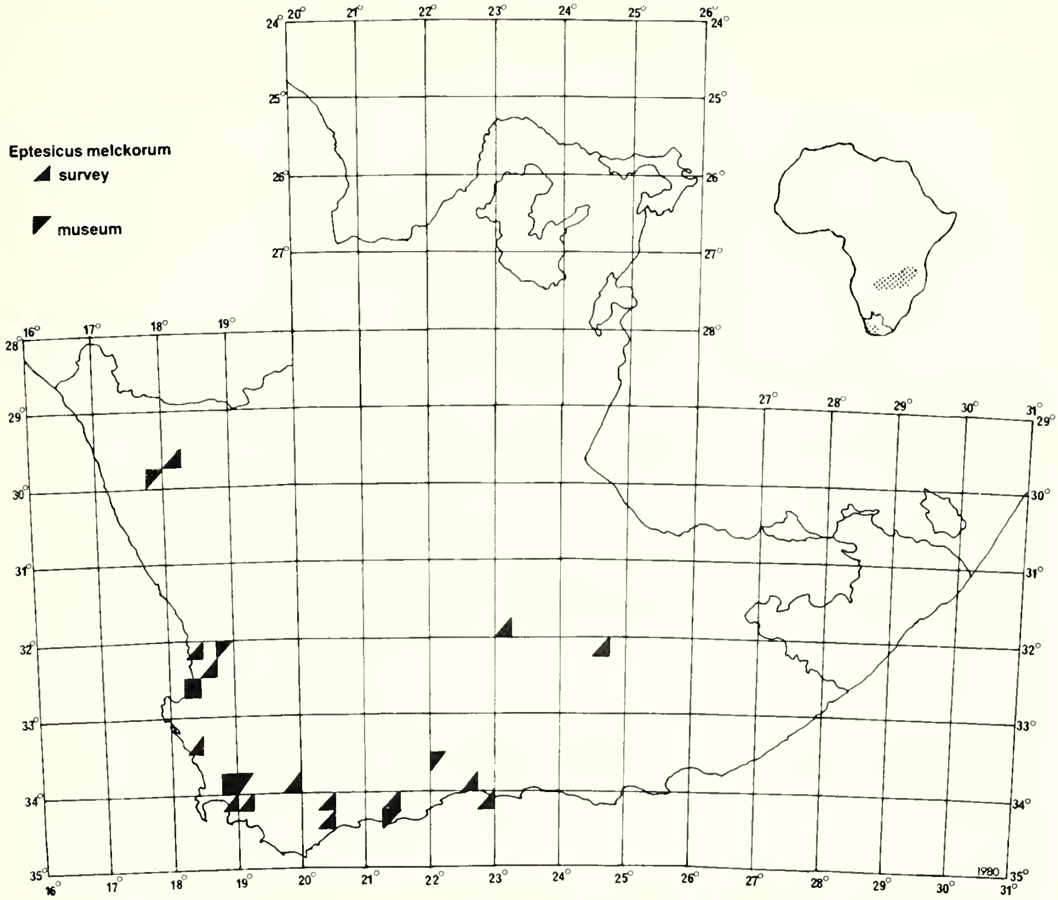

Fig. 14. The distribution of *Eptesicus melckorum* in the Cape Province.

Eptesicus melckorum Roberts, 1919 — Melck's House Bat

Eptesicus melckorum and *E. capensis* are very similar in outward appearance but there are marked differences in their forearm and skull measurements. At Herbertsdale and Vrolijkheid both species were found together in roofs.

Distribution and status

Hayman & Hill (1971) mentioned five Zambian specimens as constituting the only material collected outside the Cape Province and suggested that they might belong to a local subspecies. Most other authors stated that *E. melckorum* occurs only in the south-western Cape. During the survey the majority of specimens came from this area. However, two females collected at Three Sisters and Graaff-Reinet in the Great Karoo indicate a slightly wider distribution (Fig. 14).

Within its distribution area *E. melckorum* is quite common and is usually found in hiding places in groups of several individuals.

Habits

In most cases this species was found roosting under the eaves of buildings but a few specimens were mist-netted over water in the early evening. The specimen from Three Sisters was found under the bark of a poplar tree.

Breeding

Three pregnant females, two with twin foetuses, were found at Sandberg during late October.

Material examined

Survey — 1 Aurora, 1 Bontebok Park, 1 Bot River, 4 Compagnies Drift, 2 De Hoop, 1 Ebb-and-flow, 1 Graaff-Reinet, 1 Goukamma, 2 Herbertsdale, 2 Hester Malan, 1 Jonkershoek, 2 Rocherpan, 3 Sandberg, 1 Strand, 1 Three Sisters, 4 Vrolijkheid, 2 Ysterfontein.

Museums — 2 Berg River, 1 Norap, 1 Stilbaai (TM); 1 Assegaaibosch, 1 Clanwilliam, 1 Rocherpan (SAM); 1 Compagnies Drift, 1 Oudtshoorn (AM).

Eptesicus capensis (A. Smith, 1829) Cape Serotine

Roberts (1951), Ellerman *et al.* (1953) and Meester *et al.* (1964) list three subspecies of this bat, of which only *E. c. capensis* occurs in the Cape. However, Meester *et al.* (1964) state that the subspecies need revision, particularly with respect to their geographic ranges and Hayman & Hill (1971) do not recognize any separate subspecies.

Distribution and status

E. capensis is fairly common throughout the Cape Province (Fig. 15) and a number of individuals are usually found together in each roost. Because of its habit of roosting in houses it is one of the few bat species that may have increased in numbers as a result of man's acivities.

Habits

In the majority of cases *E. capensis* was found hiding in small crevices under the eaves of buildings. On a few occasions specimens were netted over water. At Brandvlei one specimen was taken from wool-bags hanging from the roof of a garage.

Breeding

Pregnant females were collected in early November at Barkley West and juveniles were found in late November at Barkly East.

Material examined

Survey — 1 Barkley East, 6 Barkly West, 5 Bontebok Park, 1 Brandvlei, 2 Canaga, 4 Die Oog, 1 Elliot, 1 Herbertsdale, 1 P.K. le Roux Dam, 1 Riebeeck-Oos, 1 Robertson, 2 Rolfontein, 1 Steyerskraal, 3 Vrolijkheid.

Museums — 2 Keiskamspoort, 1 Kuruman, 1 Vryburg (TM); 3 Atherstone, 6 Compagnies Drift, 2 Ezelfontein, 19 Kaggasmoudt, 22 King William's Town, 2 Lady Grey, 1 Middelburg, 2 Paddagat, 4 Tambookies Drift, 3 Traveller's Rest, 13 Lambert's

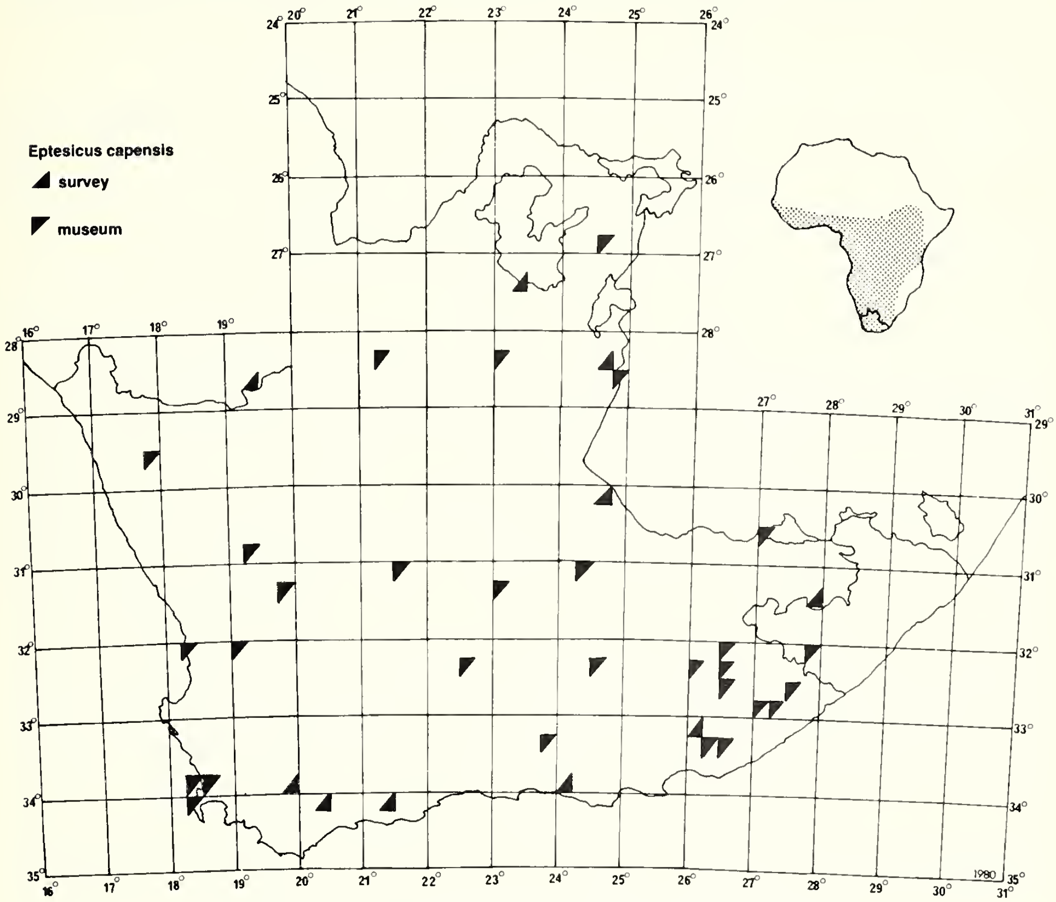

Fig. 15. The distribution of *Eptesicus capensis* in the Cape Province.

Bay, 1 Simonstown (SAM); 1 Blythswood, 1 Brakkloof, 1 Compagnies Drift, 12 Grahamstown, 2 Jameston, 1 Kaggasmoudt, 1 Kei Road, 1 Kimberley, 2 King William's Town, 2 Kleinpoort, 1 Pirie, 1 Stones Hill, 3 Victoria West, 1 Waterloo (AM).

Eptesicus notius G. Allen, 1908 — Cape Horn-skinned Bat

It is unlikely that this is a valid species. It is known only from the type specimen which was collected in Cape Town in 1908 and is now housed in the Museum of Comparative Zoology, Harvard, Massachusetts, U.S.A. Koopman (1975) considered this specimen as a slightly aberrant individual of *E. capensis*, possibly infested with nematodes, and this view is followed by Swanepoel, Smithers & Rautenbach (1980). Therefore the present authors do not consider *E. notius* as part of the Cape bat fauna.

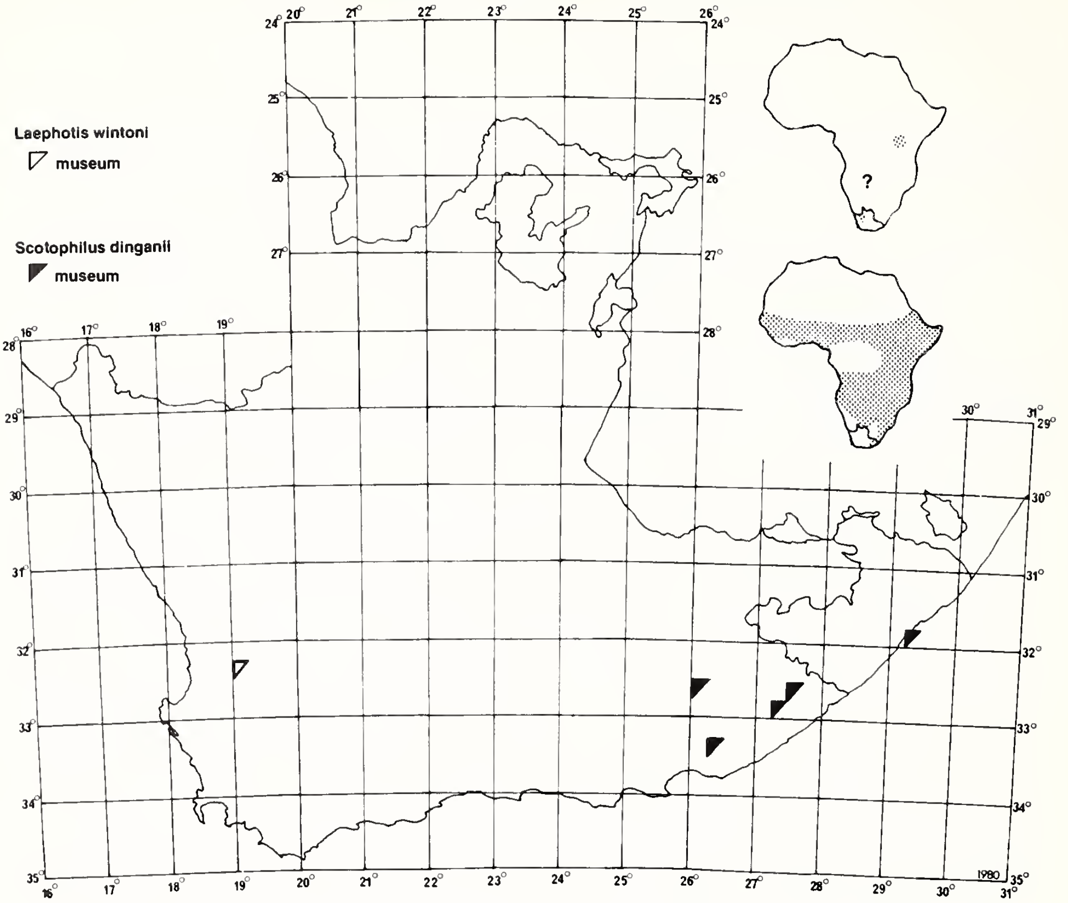

Fig. 16. The distribution of *Laephotis wintoni* and *Scotophilus dinganii* in the Cape Province.

Laephotis wintoni Thomas, 1901 — De Winton's Long-eared Bat

Bats of this genus are very rare in collections and only one specimen has been taken in the Cape Province (Rautenbach & Nel 1978). Hayman & Hill (1971) lumped all specimens under the species *L. wintoni*, but later Hill (1974) divided the genus into four distinct species with *L. wintoni* in East Africa, *L. botswanae* from Zambia and Botswana, *L. angolensis* from Angola and *L. namibensis* from South West Africa. This division was based on only 25 specimens.

In February 1978 Rautenbach & Nel (1978) netted a specimen over a river at the Algeria Forest Station in the Cedarberg (Fig. 16). These authors compared nine measurements of this specimen with those of the four known species using a multivariate analysis and came up with the rather surprising result that their specimen was by far closest to the East African *L. wintoni* which is geographically the most distant. This led them to say that the taxonomic status of the genus is not satisfactorily resolved and can only be by the acquisition of more material.

On the above evidence *Laephotis wintoni* is provisionally included in the bat fauna of the Cape Province. It is not clear whether the specimen represents a well-established local population. Because of the low number of specimens collected its status in Africa must be described as "rare" although the widespread distribution range suggests that it may occur naturally in very low numbers.

Material examined

Museums — 1 Algeria (TM).

Scotophilus dinganii (A. Smith, 1833) Yellow House Bat

The genus *Scotophilus* is characterized by having only one upper incisor, one upper premolar, three lower incisors and two lower premolars on each side. There is some confusion in its taxonomy. Robbins (1978) has shown that *S. gigas* should be called *S. nigrita* and that all specimens that have been identified as *S. nigrita* since the late 1800s must now be called *S. dinganii*. *S. dinganii* is the only species that has been collected in the Cape Province. Hayman & Hill (1971), Meester *et al.* (1964) and Roberts (1951) recognized three subspecies of what they called *S. nigrita* and stated that the subspecies *pondoensis* occurs only in the eastern Cape Province.

Distribution and status

No material was collected during the survey, but 27 museum specimens were examined (Fig. 16). All these specimens labelled as *S. nigrita*, were collected in the eastern Cape between 1931 and 1941. Recently Erasmus & Rautenbach (in press) collected a specimen in the Kalahari Gemsbok National Park which they separated from the closely related *S. viridis* using a morphometric identification model even though its colouring was more like this species than *S. dinganii*. Thus the species appears to have a very restricted distribution in the eastern and northern Cape although it is fairly widespread in Africa.

Habits

Roberts (1951) stated that this species usually lives under the eaves of buildings or in deserted nests of woodpeckers and barbets. Erasmus & Rautenbach (in press) record that their specimen was flying with several others, probably of the same species, over a drinking trough in savanna woodland.

Material examined

Museums — 1 Amabele, 3 Atherstone, 1 Kaggasmoudt, 17 King William's Town (KWT); 1 Port St Johns (SAM); 1 Gleniffer, 2 King William's Town (AM).

Kerivoula lanosa (A. Smith, 1847) Lesser Woolly Bat

This species is characterized by its long, woolly hair, 38 teeth in the dentition (the same as *Myotis*) and high cranium (similar to *Miniopterus*). Hayman & Hill (1971) question whether *K. harrisoni*, *K. lanosa* and perhaps *K. muscilla* represent distinct species or merely local forms of one widespread species.

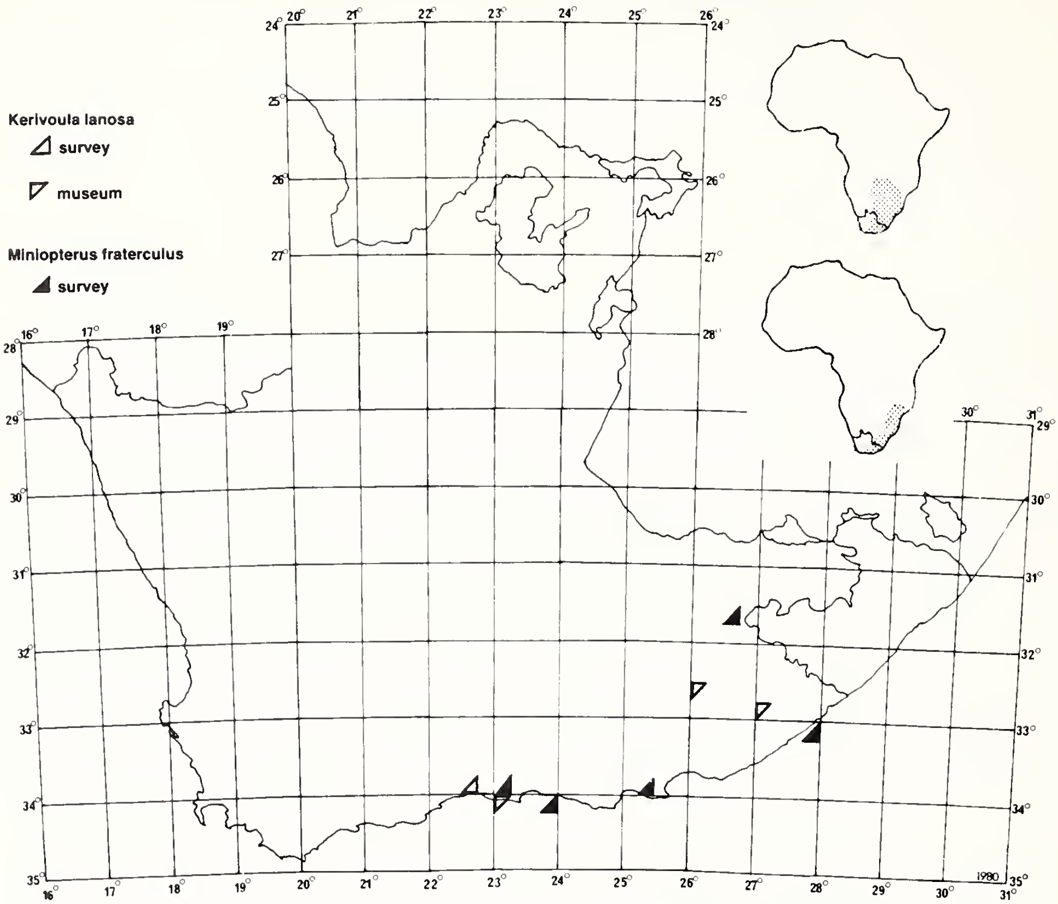

Fig. 17. The distribution of *Kerivoula lanosa* and *Miniopterus fraterculus* in the Cape Province.

Distribution and status

Seven specimens of this rare species were examined (Fig. 17). There are four museum specimens from the eastern Cape and two from Knysna in the southern Cape. During the survey one specimen was collected at Dennebos near Knysna. It appears to be restricted to the forested regions of the southern and eastern Cape. The overall conservation status of this species depends to a large extent on whether it proves to be clearly distinguishable from *K. harrisoni*.

Habits

All localities where specimens of *K. lanosa* have been collected show that the species has an affinity for forests. Roberts (1951) stated that most specimens were taken from the hanging nests of birds such as weavers.

Material examined.

Survey — 1 Dennebos.

Museums — 1 Knysna (TM); 1 Cullendale, 1 Knysna, 3 Pirie (AM).

Miniopterus fraterculus Thomas & Schwann, 1906 Lesser Long-fingered Bat

Bats of the genus *Miniopterus* are easily distinguished by the elongated second phalanx of the third digit. The four species listed by Hayman & Hill (1971) as occurring in Africa are all very similar in appearance and are usually separated on forearm and skull lengths. However, there is some overlap in both size and distribution ranges, and the taxonomy of the genus is therefore rather confused.

Hayman and Hill (1971) record two species for the Cape Province, *M. fraterculus* and *M. schreibersii*. The former is generally regarded as being smaller than the latter although the forearm length classes of 42–44 mm and 42–47 mm respectively used by Hayman & Hill (1971) cannot be considered as diagnostic characters. These authors mention that *M. fraterculus* has variously been included in *M. minor* and *M. schreibersii*. However they follow Harrison & Clancey (1952) in declaring it a separate species, without giving clear reasons for the distinction.

During the present study different forms of *Miniopterus* were found on several occasions. In large roosts of *Miniopterus* occasional individuals had a russet or partly russet colour and appeared to be smaller than the typical dark blackish-brown coloured *M. schreibersii*. These small, russet individuals were assumed to belong to *M. fraterculus*, and this identification was supported by Prof. J. Meester (pers. comm.) who examined some of the specimens. However, wet specimens were very difficult to separate and this may have led to mis-identifications in the collection.

Distribution and status

Roberts (1951) recorded *M. fraterculus* from Knysna and Hayman & Hill (1971) stated that it occurs in the eastern Cape Province, eastern Transvaal, southern Malawi and Zambia. During the survey at least eight specimens were collected at five roosts in the southern and eastern Cape but no Cape specimens were found in the museums (Fig. 17). Due to confusion with *M. schreibersii* it is difficult to assess its status. However, it does not appear to be rare in the Cape Province.

Habits

In every instance this species was found in the same roost as *M. schreibersii*. No evidence could be found of how the two species differ ecologically.

Material examined

Survey — 2 Bat's Cave, 1 Gant's Mine, 2 Millwood Mines, 2 Sterkstroom, 1 Storms River Mouth.

Miniopterus schreibersii (Kuhl, 1819) Schreibers' Long-fingered Bat

This species is by far the most abundant cave-bat found in the Cape Province, where it is represented by the subspecies *M. s. natalensis* (A. Smith, 1834).

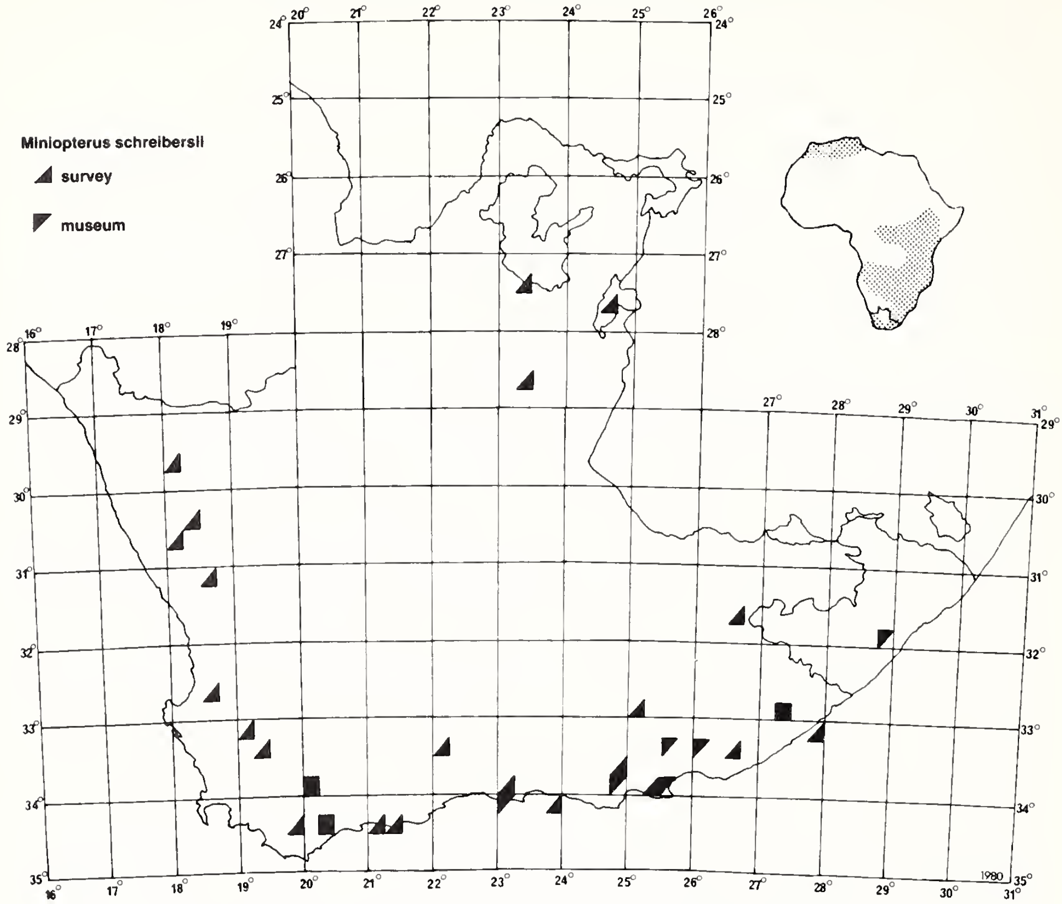

Fig. 18. The distribution of *Miniopterus schreibersii* in the Cape Province.

Distribution and status

M. schreibersii has a very wide distribution, being found in Africa, Asia and Australia. In Africa it occurs throughout the continent south of the Sahara. The subspecies *M. s. natalensis* is found from the southern Congo and Zambia southwards (Hayman & Hill 1971). It is abundant in the Transvaal (Van der Merwe 1972a) and Natal (Harrison & Clancey 1952).

During the survey large colonies were found in all regions of the Cape Province (Fig. 18). At De Hoop 157 specimens were collected for population dynamics studies, and a further 300 specimens were collected from localities throughout the province.

The species is very common in the Cape Province. However, its marked decline in some areas due to disturbance at the roosts gives cause for concern. This may be of considerable economic importance, since large colonies are likely to have a substantial influence on local insect populations.

Habits

Bats of this species congregate in very large colonies, especially in the nursery caves such as the De Hoop Cave where about 80 000 females form a nursery colony during the summer months. They migrate seasonally and banding studies have shown that individuals migrate at least 250 km to and from De Hoop every year (Herselman & Norton in prep.). As found by Van der Merwe (1973b, 1973c, 1975) and Norton & Van der Merwe (1978) in the Transvaal, these movements appear to be associated with the selection of suitable sites for winter hibernation.

Within roosts these bats gather in large densely-packed clusters. Densities of up to 2 800 individuals/m^2 have been estimated by Norton & Van der Merwe (1978). *M. schreibersii* is often found in association with other bat species especially, *Rhinolophus clivosus, R. capensis* and *Myotis tricolor*.

Breeding

Of the 170 females examined at De Hoop in October 158 (93%) were pregnant. Parturition took place from the end of October to the middle of November. The infants were left in dense clusters against the walls while the females fed or rested in the cave. There is some evidence that females suckle offspring other than their own, since a pregnant female suckling an infant was collected. Twinning is rare and was found in only one out of more than 150 pregnant females dissected.

During the survey only four nursery caves were located, at De Hoop in the south-western Cape, Koegelbeen Cave in the northern Cape, Bloukrans Cave in the Karoo, and the disused Maitland Mines in the eastern Cape. These nursery caves are considered to play an important role in the survival of the species.

Material examined

Survey — 9 Bat's Cave, 28 Bean-se-bos, 21 Bloukrans, 157 De Hoop, 3 Die Oog, 18 Die Hel, 1 Droëvlakte, 49 Gant's Mine, 4 Goegab, 1 Grahamstown, 1 Hansies River Mine, 1 Hot Pot, 1 King William's Town, 22 Koegelbeen Cave, 8 Marcus Mud Crawl, 8 Millwood Mines, 52 Montagu Cave, 3 Nabeeb Mine, 4 Norlim Mine, 2 Orrelgat, 1 Puntjie Cave, 22 Roodebergskloof, 10 Skrik van Rondom, 2 Skurweberg Cave, 17 Sterkstroom, 4 Storms River Mouth.

Museums — 3 Knysna, 3 Table Mountain (TM); 69 King William's Town, 1 Patensie, 1 Schoenmakerskop (KWT); 2 De Hoop, 1 King William's Town, 1 Knysna, 1 Wynberg (SAM); 4 Buffelskloof, 1 Dunbrody, 1 Gleniffer, 4 King William's Town, 6 Mqanduli, 1 Redhouse, 11 Slaaikraal (AM).

Family MOLOSSIDAE

Sauromys petrophilus (Roberts, 1917) — Roberts' Flat-headed Bat

As the common name suggests the skull of this bat is conspicuously flattened, a characteristic which clearly separates it from species of *Tadarida*, the other free-tailed genus. When originally describing it, Roberts (1917) placed it under *Platymops* with *Sauromys* as a subgenus, but *Sauromys* has now been elevated to generic rank (Hayman & Hill 1971). The genus as a whole is limited to southern Africa.

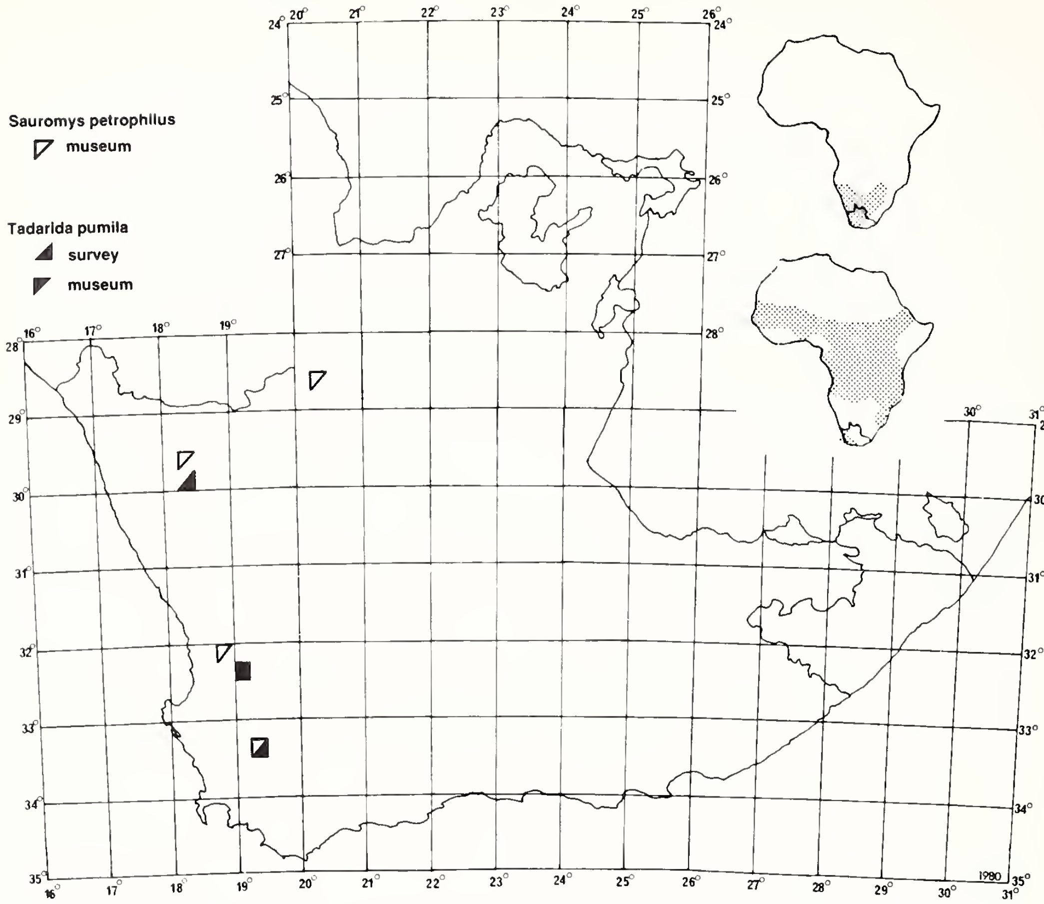

Fig. 19. The distribution of *Sauromys petrophilus* and *Tadarida pumila* in the Cape Province.

Distribution and status

During the survey no specimens of this species were collected. Only eight museum specimens were located bearing out the statement of Hayman & Hill (1971) that flat-headed bats are not numerous in collections.

All the specimens are from the south-western Cape and Namaqualand (Fig. 19), and all, except those from Augrabies Falls, were collected before 1940, suggesting that the species is very rare in the Cape. However, the main reason for their scarcity seems to be that they have very specific habitat requirements and Rautenbach (pers. comm.), who collected the two Augrabies Falls specimens in 1970 and 1977, is of the opinion that they will prove to be more widespread if more intensive searches are made in areas with suitable habitats.

Habits

The flattened heads of these bats enable them to roost in very narrow crevices between rocks, where they usually occur singly or in pairs (Smithers 1971).

Material examined

Museums — 2 Augrabies Falls, 1 Michell's Pass (TM); 1 Clanwilliam, 4 Goodhouse (KWT).

Tadarida condylura (A. Smith, 1833) Angola Free-tailed Bat

Roberts (1951), Ellerman *et al.* (1953), Meester *et al.* (1964) and Hayman & Hill (1971) state that this free-tailed bat occurs from the eastern Cape Province northwards over a large part of Africa. However, during the survey no specimens were collected and no material from the Cape Province was found in the South African museums. Since a large proportion of the eastern Cape has been excised to form Transkei it is quite likely that this marginal species does not occur within the present borders of the Cape Province.

Tadarida pumila (Cretzschmar, 1826) Little Free-tailed Bat

As suggested by the common name this species is noticeably smaller than any other free-tailed bat in the Cape Province.

Distribution and status

Before the survey the little free-tailed bat was only recorded from the eastern parts of southern Africa. However, in February 1978 a series of 13 specimens, all females, was mist-netted over water by Rautenbach & Nel (1978) at the Algeria Forest Station in the Cedarberg. During the present survey a single female was collected in August 1978 from a farm dam at Goegab near Springbok. In September 1979 a series of 10 specimens was mist-netted in the same place. During the same month two males and a female were caught at Algeria and another female was caught at Michell's Pass near Ceres.

The range of this species therefore seems to be greater than originally described, probably extending southwards along the mountain chains of the south-western Cape Province (Fig. 19). The present study also refutes the idea of sex segregation mentioned by Rautenbach & Nel (1978). The rate of success with mist-netting suggests that the species may be more common in the western Cape than was previously thought.

Material examined

Survey — 3 Algeria, 11 Goegab, 1 Michell's Pass.

Museums — 13 Algeria (TM).

Tadarida aegyptiaca (E. Geoffroy, 1818) Egyptian Free-tailed Bat

This is the largest free-tailed bat in the Cape Province. Roberts (1951) recognizes. *T. aegyptiaca* and *T. bocagei* as distinct species, but Hayman & Hill (1971) regard *T. a. aegyptiaca* and *T. a. bocagei* as two subspecies of *T. aegyptiaca*, with the slightly smaller and darker *T. a. bocagei* occurring in the drier western parts of southern Africa.

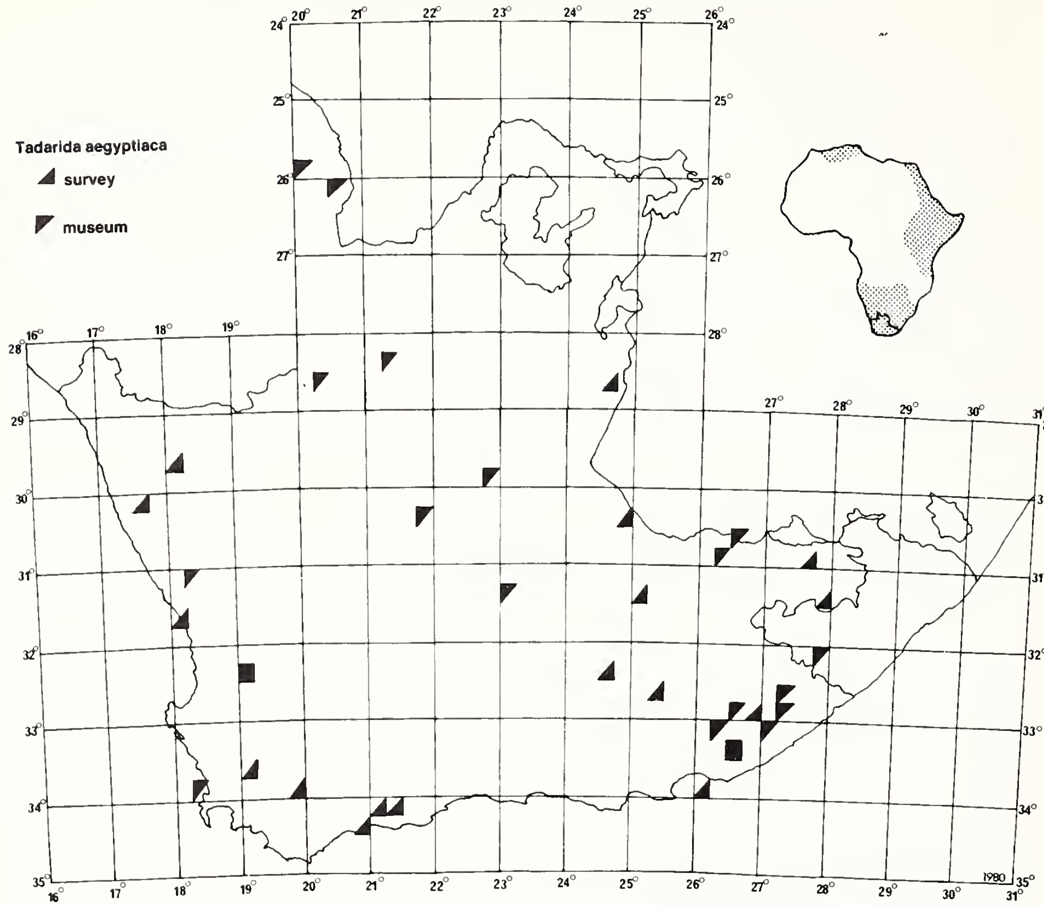

Fig. 20. The distribution of *Tadarida aegyptiaca* in the Cape Province.

Distribution and status

According to earlier authors *T. aegyptiaca* occurs all over the Cape Province and over the greater part of the continent. The present survey confirmed its wide distribution in the province (Fig. 20), showed that it is fairly common throughout, and has several large colonies of a few hundred individuals. Its conservation status appears to be secure. Its habit of roosting in buildings, especially churches, suggests that it is one of the few insectivorous species to have benefitted from man's activities.

Habits

Colonies were found in cracks between rocks. *T. aegyptiaca* also congregates in crevices in buildings. It has a strong musky odour. As suggested by Shortridge (1942) it is seldom associated with other bats, although at Herbertsdale it was found in the same roof as *Eptesicus*

capensis. It appears to congregate to breed, as indicated by the fact that a series of 10 specimens from Junction Farm consists only of pregnant females collected from clefts in rocks near waterholes.

Breeding

Heavily pregnant females were found at several localities during November, suggesting that births take place towards the end of November or the beginning of December.

Material examined

Survey — 1 Abraham Kriel, 10 Algeria, 1 Aronegas, 2 Barkly East, 3 Cape Infanta, 2 Doringbaai, 3 Elliot, 4 Goegab, 1 Graaff-Reinet, 1 Grahamstown, 2 Herbertsdale, 1 Herbertshope, 10 Junction Farm, 3 Middelburg, 3 Riversdale, 1 Rolfontein, 2 Wellington, 2 Wilgerfontein, 1 Vrolijkheid.

Museums — 4 Algeria, 1 Augrabies Falls, 1 Burgersdorp, 2 Kamferboom, 1 Twee Riviere, 2 Van Wyksvlei (TM); 3 King William's Town, 3 Upington (KWT); 1 Cape Town, 2 King William's Town, 1 Pirie (SAM); 2 Aliwal North, 1 Blythswood, 1 Fort Beaufort, 7 Grahamstown, 3 King William's Town, 10 Middleton, 1 Peddie, 1 Victoria West, 7 Waterloo (AM).

DISCUSSION

During the survey a considerable amount of information was gathered on the occurrence and numbers of bats in the Cape Province, especially of the communal species which congregate in large roosts. However, the conservation status of many species is still not clear. There are four main reasons for this. Firstly, the taxonomy of several species or groups of species is rather confused. Secondly, the excision of Transkei from the Cape Province excludes most of the known range of several of the marginal tropical species from the eastern Cape. Thirdly, a far more intensive netting programme will have to be carried out to form an accurate picture of the solitary species, which may naturally occur in rather low densities. Fourthly, although some of the communal species may be abundant, it was difficult to show whether they were maintaining their numbers or declining.

To determine the distribution and status of a species it is essential to be able to separate it from other closely related species. The groups of species from the Cape that need to be examined more closely in order to resolve taxonomic problems involving such differentiation are: *Myotis seabrai* and *M. lesueuri*; the four species of the genus *Laephotis*; *Rhinolophus denti* and *R. swinnyi*; *Kerivoula lanosa* and the East African *K. harrisoni*; *Rhinolophus clivosus*, *R. capensis* and *R. darlingi*; and the two *Miniopterus* species, *M. schreibersii* and *M. fraterculus*. The last two groups deserve special attention because they show some overlap in the diagnostic characters used and furthermore often occur together in large colonies. Therefore a clear ecological separation will have to be documented before they can be convincingly identified as distinct species.

A further pair of species that seems to have been confused is *Pipistrellus nanus* and *P. kuhlii*. Initially the authors also found it difficult to separate them using the key in Hayman & Hill (1971), but later found they could be clearly separated on skull characters.

Other problems caused by mis-identifications are the records of *Eptesicus notius* and *Nycteris hispida* in the Cape. *E. notius* is now generally considered invalid as a species, being merely an aberrent *E. capensis*. The record of *N. hispida* is based on a single specimen that was found with several *N. thebaica* adults and was most probably a juvenile of this species.

Whether or not species are endemic to the Cape Province also depends upon taxonomic interpretation. *Myotis lesueuri* is recorded as endemic to the Cape but, if it proves to be conspecific with *M. seabrai*, its range is somewhat greater. Although *Kerivoula lanosa* is listed only from the Cape Province in Hayman & Hill (1971), Rautenbach (1982) and Smithers (1983) record it from the Transvaal and other areas in southern Africa. If it proves to be conspecific with *K. harrisoni*, the species' distribution range will include a large part of Africa. There is too much disagreement on the taxonomy of African bats at the subspecific level for it to be possible at present to reach a conclusion about the presence of endemic subspecies in the Cape Province.

Table 1 summarizes what is known of the conservation status of bats in the Cape Province. It shows that 16 species can be considered as rare in the province. This number can be divided into two groups, those that are only marginally distributed and those that are nowhere common. The excision of part of the eastern Cape to form Transkei has affected the status of the marginal tropical species in the Cape Province. Of these *Hipposideros caffer* and *Tadarida condylura* had only been recorded from what is now Transkei. At present it seems doubtful whether *T. condylura* occurs within the present borders of the province. During the survey *H. caffer* was recorded from the north-western Cape which means that the species can still be considered as part of the Cape bat fauna.

Because this study concentrated on the roosts of communal species insufficient data were gathered on the solitary species to determine their true conservation status. Of the 16 species listed as rare in Table 1, nine are nowhere common and may naturally occur at low densities. Most of them appear to have specialized habitat requirements and consequently have seldom been collected. This has resulted in the taxonomic confusion of many of the rare species. The authors are fairly confident that an intensive netting progamme, especially in the drier areas of the Karoo and Namaqualand, would show several of the "rare" species to be fairly common within a restricted habitat.

It is difficult to say whether there has been any great change in distribution and status of the more solitary species in recent years, mainly because so little netting has been carried out. What is needed is an intensive netting programme in all of the localities where "rare" species have been collected in the past and then selective trapping for particular species in similar habitats where they are likely to occur.

Since most of the more solitary species occur in low densities and in scattered roosts there seems to be little that can be done to conserve them at this stage. The major threats are insecticides and unnecessary killing by people. Therefore the priorities are an insecticide testing programme to monitor the effects of pesticides and public education to create a greater awareness of the value of bats in nature.

The more gregarious bat species, which gather in large colonies, are in a very different position. Not only is it known that in some places, such as the Kalk Bay Caves on the Cape Peninsula and the Cango Caves near Oudtshoorn, large colonies have almost disappeared but it is possible to take active steps to prevent further damage in other areas where large colonies are still to be found.

TABLE 1

Summary of specimens and known conservation status of bats in the Cape Province

Species	*Survey Specimens*	*Specimens in S.A. museums*	*Conservation status*
Epomophorus wahlbergi	7	142	FAIRLY COMMON in the S.E. and E. Cape.
Epomophorus crypturus	1	—	RARE, marginal in the E. Cape coastal belt but common elsewhere in Africa.
Eidolon helvum	1	5	RARE migrant in N. Cape but common elsewhere in Africa.
Rousettus aegyptiacus	20	35	COMMON in S.W., S. and S.E. coastal regions.
Taphozous mauritianus	—	2	RARE in S. and E. Cape but widespread in Africa.
(Nycteris hispida)	—	—	NOT PRESENT—incorrect identification.
Nycteris thebaica	43	121	FAIRLY COMMON throughout.
Rhinolophus fumigatus	—	—	VERY RARE, marginal in N.W. Cape but widespread in Africa.
Rhinolophus darlingi	4	30+	UNCOMMON in N. Cape, but probable confusion with next two species.
Rhinolophus clivosus	133	77	COMMON in coastal areas and N. Cape.
Rhinolophus capensis	157	120	FAIRLY COMMON in coastal areas, possibly endemic to Cape Province.
Rhinolophus denti	—	—	VERY RARE, old records only for the Cape, restricted distribution in southern Africa. Possibly conspecific with next species.
Rhinolophus swinnyi	—	20	RARE, old records only for the Cape, restricted distribution in southern Africa.
Hipposideros caffer	2	26	RARE, marginal in N.W. & E. Cape but more common elsewhere in Africa.
Myotis seabrai	5	8	VERY RARE in N.W. Cape, restricted distribution on W. coast of southern Africa. Possibly conspecific with next species.

Species	*Survey Specimens*	*Specimens in S.A. museums*	*Conservation status*
Myotis lesueuri	2	3	VERY RARE ENDEMIC, scattered records from Karoo, N. & S.W. Cape.
Myotis tricolor	44	16	UNCOMMON in S.W., S. & E. Cape but widespread up E. coast of Africa.
Pipistrellus nanus	—	4	RARE, marginal in E. Cape, old records only but common elsewhere in Africa.
Pipistrellus kuhlii	—	3	RARE, marginal in E. Cape, old records only but widespread in Africa.
Eptesicus hottentotus	6	7	RARE in W. & N.E. Cape, restricted distribution in southern Africa.
Eptesicus melckorum	30	9	FAIRLY COMMON in Karoo, S.W. & W. Cape, otherwise restricted distribution in Angola & Zambia.
Eptesicus capensis	30	122	COMMON throughout.
(Eptesicus notius)	—	—	INVALID SPECIES.
Laephotis wintoni	—	1	VERY RARE, only one specimen from S.W. Cape. Taxonomy unclear.
Scotophilus dinganii	1	26	RARE, marginal in E. Cape, historical records only, but widespread in Africa.
Kerivoula lanosa	1	6	VERY RARE in S. & E. Cape, restricted distribution in southern Africa, but taxonomy needs attention.
Miniopterus fraterculus	8	—	UNCOMMON in S. & E. Cape, although confusion with next species; taxonomy needs attention.
Miniopterus schreibersii	470	159	VERY COMMON throughout, apart from central Karoo.
Sauromys petrophilus	—	8	RARE in W. Cape and restricted in southern Africa.
(Tadirada condylura)	—	—	Probably NOT PRESENT, marginal in Transkei.
Tadarida pumila	15	13	UNCOMMON in W. Cape but only recently discovered and little known, widespread in Africa.
Tadarida aegyptiaca	53	61	Common throughout.

TABLE 2:

The most important bat roosts known in the Cape Province, with the estimated maximum number of bats seen (seasonally numbers may be lower due to migration)

Roost	*Max. No. of bats*	
(1) De Hoop Cave (Bredasdorp)	100 000	*Miniopterus*
	12 000	*Rhinolophus*
	2 000	*Myotis*
	100	*Nycteris*
(2) Koegelbeen Cave (Griquatown)	60 000	*Miniopterus*
	5 000	*Rhinolophus*
(3) Maitland Mines (Port Elizabeth)	8 000	*Miniopterus*
	1 500	*Myotis*
	200	*Rhinolophus*
(4) Die Hel Cave (Groot Winterhoek)	4 000	*Miniopterus*
	2 000	*Rousettus*
	1 500	*Rhinolophus*
	100	*Myotis*
(5) Bloukrans Cave (Pearston)	4 000	*Miniopterus*
	1 000	*Rhinolophus*
(6) Montagu Cave (Montagu)	5 000	*Miniopterus*
(7) Bean-se-bos (Hankey)	1 500	*Miniopterus*
	1 000	*Rousettus*
	500	*Rhinolophus*
(8) Welbedacht Mine	3 000	*Miniopterus*
(9) Droëvlakte Cave	1 500	*Miniopterus*
	1 000	*Rhinolophus*
(10) Sterkstroom Mine	1 000	*Miniopterus*
	1 000	*Rhinolophus*
(11) Storms River Mouth	2 000	*Rousettus*
(12) Forest Ranch	1 000	*Nycteris*
	500	*Rhinolophus*

Roost	*Max. No. of bats*	
(13) Grootplaas Cave	1 000	*Rhinolophus*
(14) Helderberg Cave	500	*Rousettus*
(15) Wellington Church	300	*Tadarida*

Table 2 gives the approximate numbers of individuals found in the larger colonies visited during the survey (see also Fig. 2). Some of these are nursery caves which play a very important role in the survival of all species. For example, in summer the De Hoop Cave attracts about 80 000 pregnant *Miniopterus schreibersii* females from within a radius of up to 250 km. Disturbance at this critical stage can lead to a high mortality of offspring and the effective protection of such roosts is therefore of the utmost importance.

It is clear that the large numbers of bats present in these caves must have a marked effect on the insect fauna of the surrounding areas and must therefore play an important role in the ecosystem. Although it is known that certain roosts have disappeared due to disturbance it is difficult to tell at this stage whether the major roosts are maintaining their numbers or not. It is important therefore that efforts to protect the roosts be accompanied by a low intensity, low disturbance monitoring programme to determine whether conservation measures are being effective or not.

CONSERVATION OF BATS IN THE CAPE PROVINCE

The conservation of bats is dependent on a clear understanding of the legislation governing their protection.

The Nature Conservation Ordinance (No. 19 of 1974) of the Cape Province lists three categories of protection for all indigenous wild animals. These are 'Endangered Wild Animals' (Schedule 1 of the Ordinance), 'Protected Wild Animals' (Schedule 2), and 'Wild Animals' for all other indigenous species. All bats are therefore 'Wild Animals' and all insectivorous bats (Microchiroptera) are classified as 'Protected Wild Anmimals'. The reason for the exclusion of fruit bats (Megachiroptera) from Schedule 2 is that they are considered to be potential problem animals because of the damage that they sometimes cause to fruit crops.

There are several restrictions on how all wild animals may be killed or hunted. As 'Wild Animals' no bats may be hunted using prohibited methods (Section 29 of the Ordinance) unless the 'hunter' is the holder of a permit authorizing him so to do. This means that he may not use poison, artificial lights or any type of trap (including nets), and he may not hunt at night. Written permission from the owner of the land is also obligatory.

Further restrictions (Section 27) apply to the insectivorous bats (as 'Protected Wild Animals') in that they may not be hunted, killed or captured without a permit. This includes bats caught or killed for scientific research.

In addition to the above regulations on 'hunting', no 'Wild Animals' may be kept in captivity without a permit (Section 31), and no 'Wild Animals' may be exported from, imported into or transported within the province without a permit (Section 44).

These regulations are far from adequately adhered to or enforced at present, and many bats are still killed illegally and unnecessarily.

Conservation management

For most of the solitary bat species little can be done at present for their protection. There is even little hope of enforcing the existing legislation if people are antagonistic towards them. A public awareness campaign is therefore the only long-term solution. Such a campaign should aim to persuade the public to accept the ecological and economic importance of bats and to discourage all forms of disturbance. Initially the most effective way to reduce antagonism towards bats in general is to give good advice on how to avoid problems with roof-dwelling bats and to quell rumours that bats are major carriers of rabies.

For the colonial species considerably more can be done. The effective protection of *all* large colonial roosts should be given highest priority in bat conservation. This involves both the enforcement of the regulations on the killing of bats and the reduction of disturbance during critical periods.

Legislation

Whereas legislation to control the killing of bats is adequate at this stage, consideration should be given to including the fruit bats (Megachiroptera) in Schedule 2 as 'Protected Wild Animals'. This would mean that a permit would have to be obtained under Section 47 of the Ordinance before fruit bats could be destroyed or captured. This should not prevent farmers from protecting their crops as permits should be freely issued where damage is being done. However, it would emphasize to farmers that fruit bats are an important part of natural ecosystems and that indiscriminate killing is not supported. The main advantage of the permit system is that it makes it possible to monitor the extent and severity of the problem in the province and thereby to put into a clearer perspective the often exaggerated claims of damage done by fruit bats. A similar system is already in operation for small antelope such as grysbok and duikers which occasionally cause similar localized and seasonal problems.

Research

There are two main priorities for further research on bats in the Cape Province. The first is that work should be done on the distribution and taxonomy of the more solitary species occurring in the province. This would involve an extensive netting programme, especially in the Karoo and northern parts of the province. It should aim at concentrating on particular species, at following up old records of the occurrence of a species at sites at which collecting has not recently taken place, and also at looking in habitats known to be suitable for scarce species.

The second research priority should be to determine whether bats in various areas are being markedly affected by pesticides. This would involve chemical analysis of pesticide residues in small samples of bats from areas in which they are most likely to be affected. If significant residues are found, this programme could be expanded to form a full scale research and management project. If no significant residues are found, the information would serve as useful base line data for a low intensity long-term monitoring programme to detect if the use of pesticides becomes of importance to bats in the future.

Monitoring programme

A very important aspect of bat conservation that should receive attention is the establishment of a long-term monitoring programme for as many of the larger roosts as possible. The information collected should be a total count that is as precise and repeatable as possible to detect changes in the numbers of bats in the different roosts. A maximum intensity of two visits to each roost per year, in summer and in winter, is envisaged.

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Appendix: Gazetteer of localities mentioned in the text. For survey localities the co-ordinates are given where possible.

Locality	*Locus*	*Co-ordinates*	
Abbotsbury	3224 BA		
Abraham Kriel	2824 DA	28° 31′S	24° 31′E
Abrie	3322 AC	33° 22′S	22° 08′E
Algeria	3219 AC	32° 22′S	19° 03′E
Alice	3226 DD		
Alicedale	3326 AC		
Alice Mission	3226 DD	32° 46′S	26° 50′E
Aliwal North	3026 DA		
Amabele	3227 DA		
Amalinda	3227 DD	32° 59′S	27° 51′E
Apies River Forestry Station	3325 CB	33° 43′S	25° 19′E
Aronegas	3017 BA	30° 05′S	17° 42′E
Assegaaibosch	3318 DD		
Atherstone	3326 AD		
Augrabies Falls	2820 CB		
Aurora	3218 CB	32° 38′S	18° 28′E
Bakleisdrif	3420 BA	34° 05′S	20° 30′E
Balossi	3129 BA		
Barkley East	3027 DC	30° 58′S	27° 35′E
Barkly West	2824 BC	28° 30′S	24° 33′E
Bat's Cave	3327 BB	33° 05′S	27° 56′E
Bean-se-bos	3324 DB	33° 42′S	24° 49′E
Beaufort-Wes	2923 BA		
Bedford	3226 CA		
Berg River	3320 CC		
Blaney	3327 DC		
Bloukrans	3225 CC	32° 46′S	25° 14′E
Blouputs	2820 CA	28° 30′S	20° 08′E
Blythswood	3227 BB		
Bontebokpark	3420 AB	34° 04′S	20° 27′E
Boomslang Cave	3418 AB	34° 07′S	18° 26′E
Bot River	3419 AA	34° 13′S	19° 12′E
Brakkloof	3326 BA		
Brandkaros	2816 BC	28° 29′S	16° 41′E
Brandvlei	3120 BB	31° 00′S	20° 51′E
Breakfast Vlei	3326 BB	33° 05′S	26° 46′E
Buffelskloof	3326 AC		
Burgersdorp	3026 CD		
Camps Bay	3318 CD		
Canaga	3324 CC	33° 49′S	24° 01′E
Cango Caves	3322 AC	33° 24′S	22° 12′E

Locality	*Locus*	*Co-ordinates*	
Cape Infanta	3420 BD	34° 28′S	20° 51′E
Cape Town	3318 CD		
Citrusdal	3219 CA		
Clanwilliam	3218 BB		
Compagnies Drift	3218 AB	32° 07′S	18° 27′E
Cullendale (Bedford)	3226 CA		
De Hoop	3420 AD	34° 25′S	20° 21′E
Dennebos	3322 DC	33° 59′S	22° 43′E
Despatch	3325 CD		
Die Hel	3319 AA	33° 05′S	19° 05′E
Die Kelders	3419 CB	34° 33′S	19° 21′E
Die Oog (Kuruman)	2723 AD	27° 27′S	23° 26′E
Doringbaai	3118 CA	31° 46′S	18° 13′E
Doringkraal	3321 CA	33° 45′S	21° 11′E
Doringpoort River	2816 DB	28° 32′S	16° 55′E
Driefontein	3118 DC	31° 51′S	18° 36′E
Droëvlakte	3421 AD	34° 24′S	21° 25′E
Dunbrody	3325 BC		
East London	3327 BB		
Ebb-and-flow	3322 DC	33° 59′S	22° 36′E
Elliot	3127 BD	31° 20′S	27° 51′E
Elsies River	3318 DC		
Ezelfontein	3018 AC		
Forest Ranch	3227 AB	32° 09′S	27° 18′E
Fort Beaufort	3226 DC		
Fort Brown	3326 BA		
Gant's Mine	3325 CD	33° 58′S	25° 17′E
Garies	3018 CA		
George	3322 CD		
Gladstone	3227 CB		
Glass Nevie	3027 DD	30° 50′S	27° 52′E
Gleniffer	3326 BC		
Glenlea (Highlands)	3326 AD		
Goegab	2918 CA	29° 41′S	18° 01′E
Goodhouse	2818 CD		
Gordon's Bay	3418 BB	34° 11′S	18° 49′E
Goukamma	3422 BB	34° 03′S	22° 56′E
Graaff-Reinet	3224 BA	32° 15′S	24° 34′E
Grahamstown	3326 BC	33° 38′S	26° 31′E
Grootkraal Cave	3322 AC	33° 24′S	22° 12′E
Grootplaas Cave	3321 DC	33° 53′S	21° 44′E
Grootvadersbos	3320 DD		
Hanover	3124 AB		
Hansies River Mine	3419 BD	34° 23′S	19° 38′E

Locality	*Locus*	*Co-ordinates*	
Hawston	3419 AD		
Heidelberg	3420 BB		
Helderberg	3418 BB	34° 02′S	18° 52′E
Herbertshope	3326 CC		
Herbertsdale	3421 BB	34° 01′S	21° 45′E
Hester Malan	2917 DB	29° 39′S	17° 59′E
Het Kruis	3218 DA		
Hex River	3319 DA		
Hex River Estate	3218 BD		
Hondeklipbaai	3017 AD		
Hot Pot	3420 AD	34° 27′S	20° 26′E
Jameston (Highlands)	3326 AD		
Jonkershoek	3318 DD	33° 58′S	18° 55′E
Junction Farm	3226 DD	32° 54′S	26° 56′E
Kaggasmoudt	3226 CA		
Kamferboom	2620BA		
Keikamspoort	2922 DD		
Kei Road	3227 DA		
Kersbos	3018 CC	30° 59′S	18° 14′E
Keurbooms Reserve	3323 CD	33° 59′S	23° 24′E
Keurbosfontein	3219 AD	32° 28′S	19° 17′E
Kimberley	2824 DB		
King William's Town	3227 CD		
Klawer	3118 DC		
Kleinpoort	3326 BB		
Klipfontein (Albertinia)	3421 BA	34° 04′S	21° 33′E
Knysna	3423 AA		
Koegelbeen Cave	2823 CB	28° 39′S	23° 20′E
Koo Cave	3319 DA	33° 39′S	19° 47′E
Krakeel River	3323 CD	33° 49′S	23° 44′E
Kroomie	3226 CD		
Kuruman	2723 AD		
Lady Grey	3027 CA		
Lambert's Bay	3218 AB		
Lessendrum (Peddie)	3327 AA		
Lourens Farm	3318 DB		
Maitland Mines	3325 CD	33° 59′S	25° 17′E
Manley flats	3326 BC		
Marcus Mud Crawl	3322 AC	33° 23′S	22° 14′E
Mazelsfontein	2923 BA	29° 01′S	23° 34′E
McGregor	3319 DD		
Michell's Pass	3319 AD		
Middelburg	3125 AC	31° 28′S	25° 01′E
Middleton	3326 AB		

Locality	*Locus*	*Co-ordinates*	
Millwood Mines	3323 CC	33° 53′S	23° 00′E
Moneysworth	3326 DA		
Montagu	3320 CC		
Montagu Cave	3320 CC	33° 50′S	20° 10′E
Mqanduli district	3128 DD		
Nabeeb Mine (Nuwerus)	3118 BA	31° 41′S	18° 37′E
Norap	2917 DD		
Norlim Mine (Taung)	2724 DA	27° 37′S	24° 37′E
Olifantskrans Tunnel	3320 CC	33° 54′S	20° 01′E
Okiep	2917 DB	29° 32′S	17° 52′E
Orrelgat	3018 AB	30° 14′S	18° 26′E
Oudtshoorn	3322 CA		
Paddagat	2917 BD		
Patensie	3324 DD		
Peddie	3327 AA		
Pirie	3227 CB		
P.K. le Roux Dam	3024 BA		
Plettenbergbaai	3423 AB		
Port Alfred	3326 DB		
Port Elizabeth	3325 DC		
Port St Johns	3129 DA		
Puntjie Cave	3421 AC	34° 22′S	21° 30′E
Rangerton	3227 CD		
Redhouse	3325 DC		
Riebeeck-Oos	3326 AA		
Riversdale	3421 AB	34° 05′S	21° 15′E
Rocherpan	3218 CB		
Robertson	3319 DD	33° 48′S	19° 53′E
Rolfontein	3024 BD		
Roodebergskloof	3018 CA	30° 30′S	18° 05′E
Ross Mission	3227 CB		
Saasveld	3322 DC		
Saldanha Bay	3317 BB		
Salem	3326 AD	33° 15′S	26° 25′E
Sandberg	3218 BC	32° 17′S	18° 35′E
Sandberg Cave	3218 BC	32° 20′S	18° 35′E
Sandile's Cave	3227 CB	32° 43′S	27° 17′E
Schoenmakerskop	3325 DC		
Sewefontein	3119 CA		
Simonstown	3418 AB		
Simon van der Stel Mine	2917 DB	29° 38′S	17° 55′E
Skeleton Cave	3322 AC	33° 22′S	22° 10′E
Skrik van Rondom	3218 DA	32° 34′S	18° 40′E
Skurweberg Cave	3319 AD	33° 25′S	19° 22′E

Locality	*Locus*	*Co-ordinates*	
Slaaikraal	3326 AD		
Spies Cave	3322 AD	33° 24′S	22° 21′E
Spitskop	3420 AD	34° 19′S	20° 23′E
Stellenbosch	3318 DD		
Sterkstroom	3126 DA	31° 33′S	26° 30′E
Steyerskraal	2819 CB		
Stilbaai	3421 AD		
Stones Hill	3326 BC		
Storms River Mouth	3423 BB	34° 01′S	23° 54′E
Strand	3418 BB	34° 06′S	18° 49′E
Swellendam	3420 AB		
Table Mountain	3418 AB		
Tambookies Drift	3226 DA		
Taung	2724 DA	27° 37′S	24° 37′E
Three Sisters	3123 CA	31° 35′S	23° 05′E
Traveller's Rest	3219 AA		
Twee Riviere	3323 DD	33° 50′S	23° 53′E
Tunnel Cave	3422 AA	34° 12′S	22° 07′E
Tylden	3227AA		
Umtata	3128 DB		
Upington	2821 AD		
Van Wyksvlei	3021 BD		
Victoria West	3123 AC		
Vrolijkheid	3319 DD	33° 55′S	19° 52′E
Vryburg	2624 DC		
Walmer	3325 DC	33° 58′S	25° 35′E
Waterloo (Grahamstown)	3326 BC		
Wellington	3319 BA	33° 38′S	19° 00′E
Welbedacht Mine	2917 DB	29° 41′S	17° 50′E
Wilgerfontein (Pearston)	3225 CB	32° 36′S	25° 19′E
Windsor Cave	3421 AB	34° 12′S	21° 18′E
Wondergat	2816 BD		
Wynberg	3318 CD	33° 59′S	18° 24′E
Ysterfontein	3318 AC	33° 20′S	18° 09′E

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Editor
Dr F.W. GESS: 1978 –

A new species of the genus *Strongylopus* Tschudi from Namaqualand, Cape Province, South Africa (Anura: Ranidae)

by

ALAN CHANNING

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ABSTRACT

Strongylopus springbokensis **sp. nov.** is described from Namaqualand. Adults resemble *Strongylopus grayii*, but can be distinguished on the basis of body proportions and the possession of a unique male call. The advertisement call, male release call and male aggression call are illustrated. Eggs are laid on land where development proceeds to the pretadpole stage without free water. The tadpole is described and the known distribution of this species is presented.

INTRODUCTION

Six species of the ranid genus *Strongylopus* Tschudi, 1838 are presently recognized (Channing, 1981). The genus is believed to have had a southern origin (Channing, 1981) and to have subsequently migrated northwards. The species comprising this genus occupy a range of habitats, from natural forest through grasslands to semi-desert.

S. grayii (Smith) is found from the Cape to the Limpopo. It is a pioneering species, frequently found in man-made habitats like dams and ditches, even breeding successfully in refuse pits. *S. fasciatus* (FitzSimons) is a widespread grassland form found from the south eastern Cape into Malawi, Zimbabwe and eastern Zambia. *S. bonaespei* is the replacement name for *S. montanus* (FitzSimons), a form found along the mountains of the south western Cape and the Cape Peninsula. *S. hymenopus* (Boulenger) is found on the upper slopes of the Drakensberg escarpment. *S. wageri* (Wager) is a forest form collected from the uplands of Natal and the Drakensberg escarpment as well as from near Sabie.

During a recent trip to Namaqualand as part of a tadpole survey, the author heard a strange frog call at Springbok and later on the farm Bovlei on top of the Kamies mountains near Leliefontein. Calling males were collected and found to superficially resemble *Strongylopus grayii*. However, morphologically they can readily be distinguished from *S. grayii*. On the basis of a unique advertisement call and differences in morphology this frog is here described as a new species.

DESCRIPTION

Strongylopus springbokensis sp. nov.

HOLOTYPE: A male in the Port Elizabeth Museum collection, PEM A963, collected 10 July 1984 by R. C. Drewes and A. Channing at Springbok in Namaqualand (2917DC). The type locality is a small dam on the southern edge of the town.

PARATYPES: Nine adults (1 female, 8 males) collected at the same time and place as the holotype, housed in the Port Elizabeth Museum (PEM A964-A968) and the California Academy of Sciences (CAS 157517–157520).

OTHER MATERIAL EXAMINED: One adult male from the farm Bovlei near Leliefontein, the highest point (alt: 1 530 m) on the Kamies mountains (CAS 157521), and two specimens from 11 km south of Kamieskroon (PEM A1274–5).

For comparative purposes, 41 specimens of *S. grayii* in the Cape Department of Nature Conservation collection, and a series of 9 *S. grayii* from Kuboos, from the Transvaal Museum collection, were examined. (Localities of these *S. grayii* are shown later). Measurements of 63 *S. grayii* from Natal (Channing, 1979) were compared to the Cape material examined in this study and found to be indistinguishable.

The holotype (Fig. 1) is an adult male with a pale yellowish-brown dorsum in life, with irregular brown markings edged with darker brown. Dorsal surface of the legs barred. A narrow pale vertebral stripe is present in some specimens in contrast to the broad vertebral stripe common in the *S. grayii* material examined from the western Cape. Venter immaculate. In preservative the colours fade but the pattern remains. The head is relatively wider and the leg shorter than *S. grayii*. The ratios of head width/tibia and foot/head width (Fig. 2) illustrate this diagnostic difference. The snout is sharp in profile compared with that of *S. grayii* (Fig. 3).

Males in breeding condition have small sharp asperities along the posterior surfaces of the legs, and marginated fingers giving especially the first finger a paddle-like appearance. Four phalanges of fourth toe free of web.

DISTRIBUTION

The localities of specimens examined and identified as either *S. grayii* or *S. springbokensis* are presented in Fig. 4. The northernmost record for *S. grayii* is a series of animals collected at Kuboos (2816BD) in 1933. This may represent a record of a transient population which moved up the drainage lines from the Orange River during a wet period. Further collecting in the Richtersveld during the rainy season is required. Specimens of *S. grayii* collected at Wuppertal near Clanwilliam (3218BB) are morphologically intermediate between *S. grayii* and *S. springbokensis* in terms of head width and leg length. The advertisement call of the Wuppertal specimens, however, is the typical "click" of *S. grayii*.

S. springbokensis appears to be confined to the mountainous areas of Namaqualand, north of the Knersvlakte and south of the Orange River.

VOCALIZATIONS

ADVERTISEMENT CALL

The male advertisement call (Fig. 5A) consists of a series of two to seven or more notes. Each note has a duration of 0,11 s with a pulse rate of 185/s and emphasized frequencies of 0,8;

TABLE 1.

Measurements of the holotype and paratypes of *Strongylopus springbokensis*. Head length is measured from the angle of the jaw to the tip of the snout; head height is measured at the level of the tympanum. Eye and tympanum are horizontal distances. The foot includes the metatarsal tubercle and the fourth toe, while the hand includes the metacarpal tubercle.

Cat. number	PEM A963 Holotype	PEM A964	PEM A965	PEM A966	PEM A967	PEM A968	CAS 157517	CAS 157518	CAS 157519	CAS 157520
Sex	M	F	M	M	M	M	M	M	M	M
Snout-urostyle	42,0	43,5	41,3	36,2	37,1	39,4	37,3	38,2	36,3	39,6
Head width	16,2	17,5	17,1	15,5	15,7	16,5	15,4	15,6	15,4	16,0
Head length	17,0	16,1	16,3	15,2	15,3	16,0	15,4	15,6	15,2	16,1
Head height	7,6	8,6	8,2	7,0	7,2	7,4	7,7	7,4	7,2	7,0
Eye	4,4	5,0	4,8	4,1	4,4	4,6	4,3	4,7	4,3	4,4
Tympanum	2,5	2,7	3,1	2,7	2,8	2,5	2,6	2,7	3,2	2,7
Tibia	23,0	22,8	22,1	19,6	19,7	21,2	20,0	21,4	19,9	21,2
Foot	32,0	31,4	31,0	27,0	27,7	29,2	27,7	30,5	28,5	30,1
Toe	22,4	22,6	21,2	19,5	20,2	21,0	19,5	21,4	20,3	20,3
Ulna	10,8	10,2	10,4	9,0	10,0	10,1	9,5	10,1	9,6	9,9
Hand	11,1	11,5	11,0	10,0	10,5	10,6	10,0	11,0	10,5	10,5

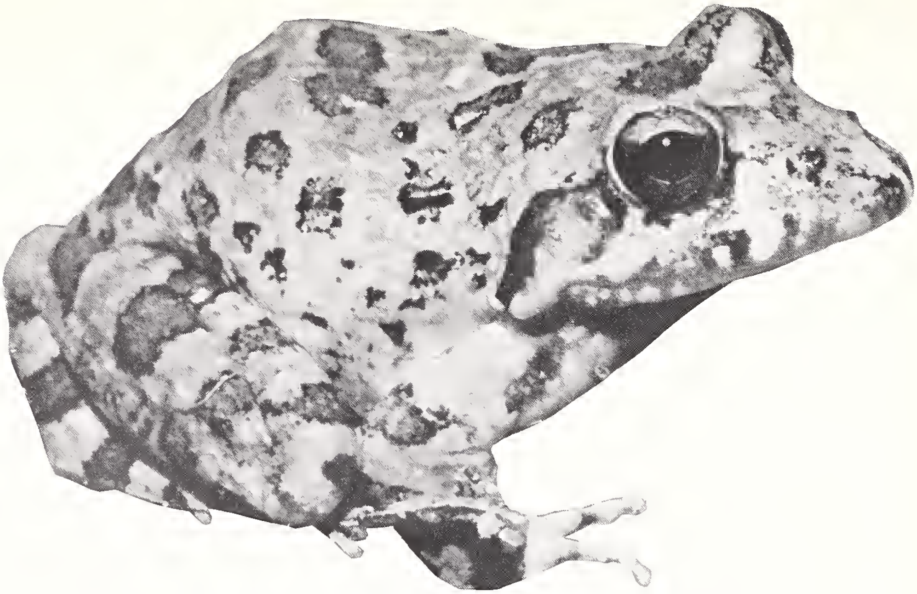

Fig. 1. Holotype of *Strongylopus springbokensis*, PEM A963.

2,6 and 3,6 kHz. Variously emphasized harmonics are visible on the sonagram from 0,8 to 8 kHz. Call duration varies from 0,22 s (two notes) to 1,17 s (seven notes). The calls described were recorded in the field at Bovlei and Springbok with a Uher CR210 cassette recorder.

MALE AGGRESSION CALL

This call (Fig. 5B) was recorded in the laboratory. It is produced when one calling male approaches another calling male. The aggression call consists of a single sharp note with an explosive burst of energy from 0,4 kHz to above 8 kHz, with the highest amplitude between 0,45 and 1,8 kHz.

MALE RELEASE CALL

The release call was recorded in the laboratory. The clasping male continues to utter the advertisement call, while the clasped male produces a long series of squeaking calls (Fig. 5C). Duration up to 3 s and probably more. Emphasized frequencies at 0,8 and 1,2 kHz.

OVIPOSITION

Eggs were first found while locating calling males in a dry stream bed below a dam wall on the farm Bovlei. The initial discovery of a disused rodent burrow serving as a call site was exciting, however, this was soon overshadowed by the discovery of the few hundred eggs found to be lining the burrow walls and floor. Other oviposition sites were subsequently located by tracing calling males, all of which were found with eggs. One such site was between grass roots in a damp crack in a rock pile. This site, like the rodent burrow, was placed about 20 cm above the dry stream bed. The eggs were found during the first week in July, at the start of the winter rain.

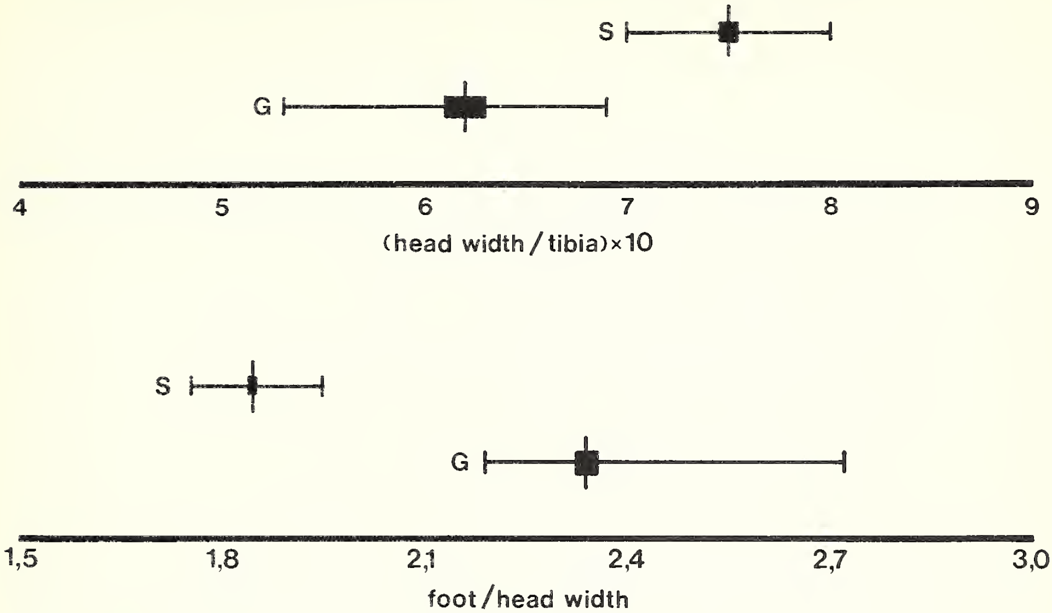

Fig. 2. Comparison of the ratios of head width/tibia and foot/head width. S = *S. springbokensis* (n = 14), G = *S. grayii* (n = 50). Range, mean and standard deviation.

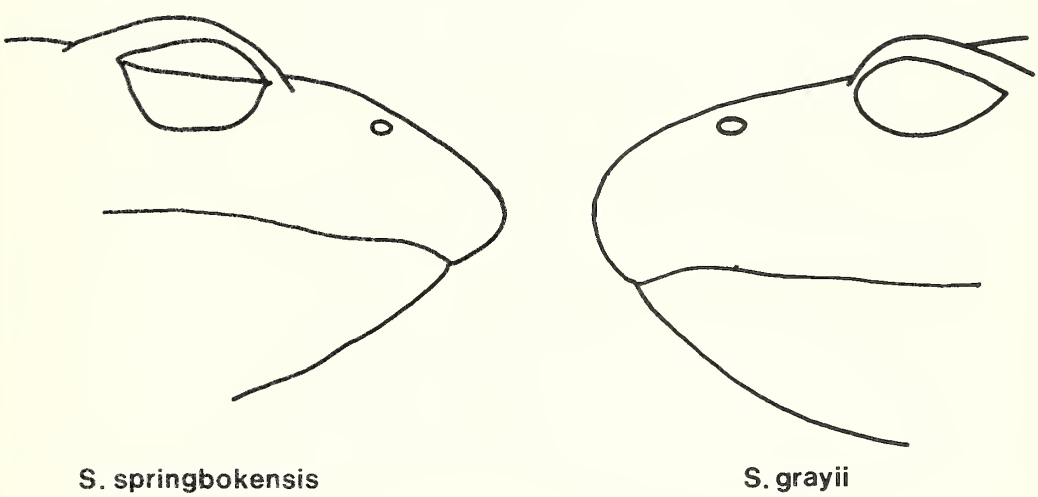

Fig. 3. Comparison of the snout profiles of *Strongylopus springbokensis* and *S. grayii* to illustrate the sharper snout of *S. springbokensis*.

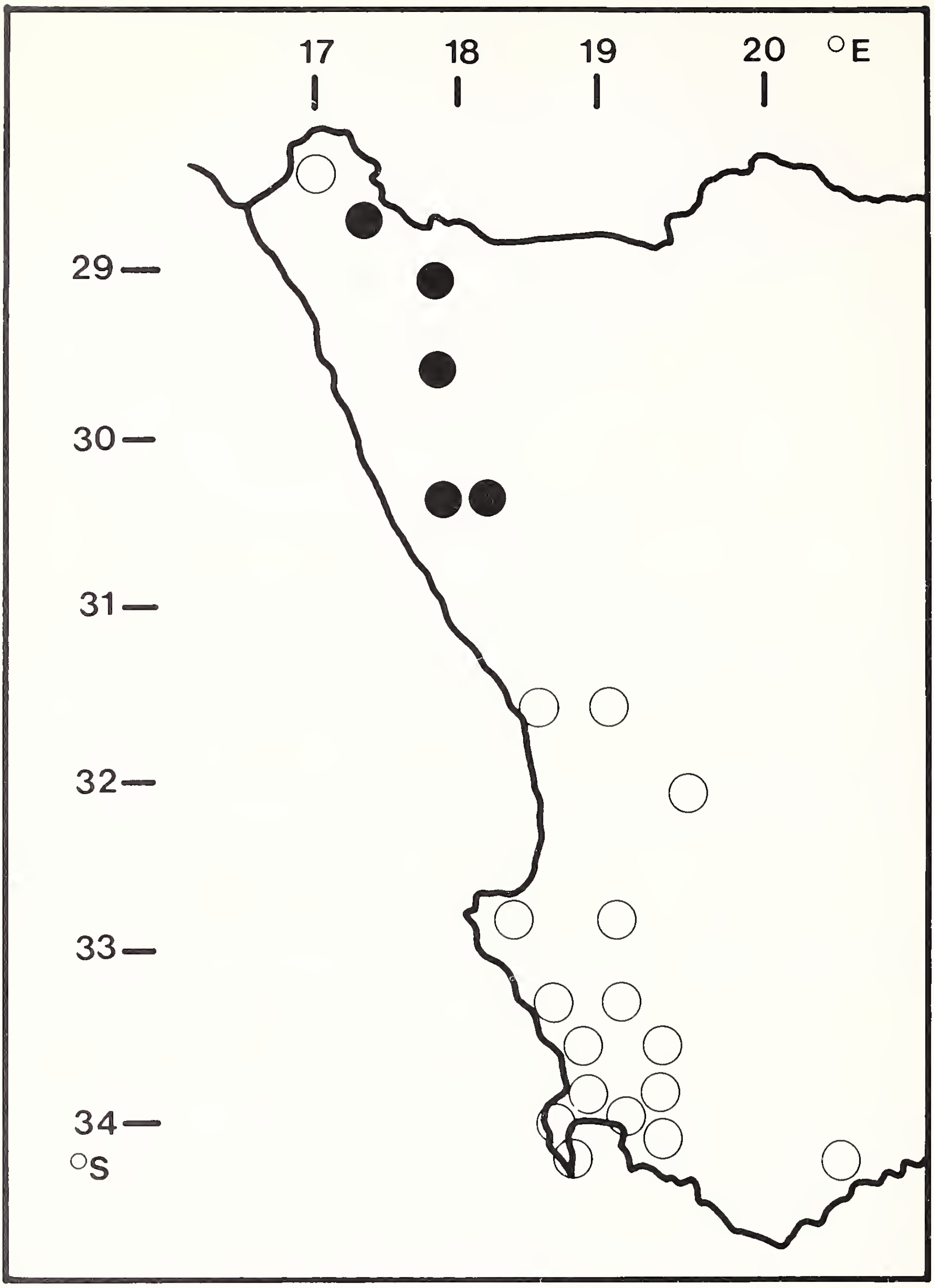

Fig. 4. Localities where *S. springbokensis* (solid circles) and *S. grayii* (open circles) are known to occur, based on material examined in the present study.

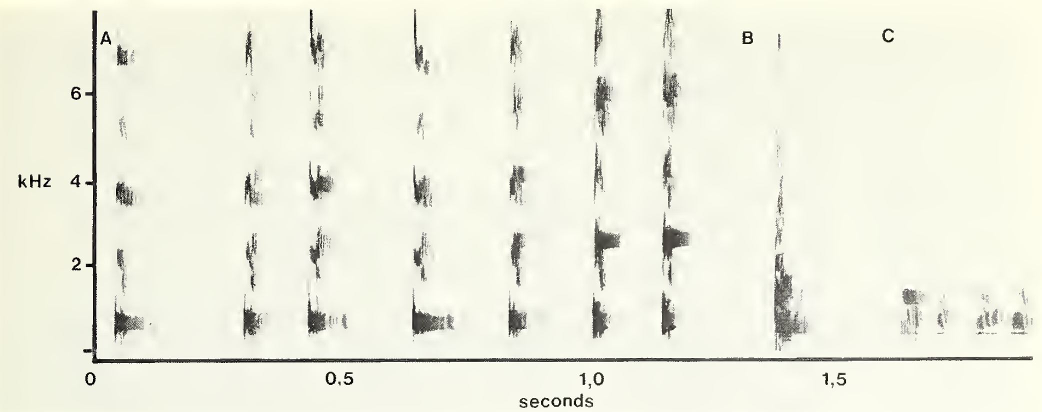

Fig. 5. Vocalizations of *S. springbokensis*. *A*—The advertisement call. *B*—The male aggression call. *C*—The male release call. Sonagrams produced with the wide filter.

A batch of eggs was found near a pool in Springbok in a grassy tunnel 15 cm above water level. Some of these eggs were placed in water immediately; these hatched within 30 minutes into free swimming tadpoles nearly 10 mm long. Part of the batch was kept for a week without water in the damp soil from the burrow where they were collected. When added to water they also hatched within 30 minutes.

From another batch 25 eggs were placed in water and observed under a microscope. They had all reached stage 22 of Gosner (1960) before being placed in water at room temperature and hatched between 20 minutes and 3 hours afterwards. The eggs seem to develop until the eyes and tail are well formed and then to remain at that stage until they are hydrated.

The independance of developing eggs from free water and the rapid hatching of well developed tadpoles soon after water is available seems to be a successful adaptation to life in the arid areas of Namaqualand.

TADPOLE

This description is based on three specimens (length 15 mm; stage 26 of Gosner (1960)) reared from eggs collected at Bovlei.

Mouth situated ventrally, not visible dorsally. Oral disc 0,85 width of head at level of disk. A single row of mental papillae. Suprarostrodont pigmented, serrated across entire margin. Infrarostrodont serrated and pigmented almost to its base.

Keratodont formula 1,3+3/1+1,2 (Fig. 6).

Nostrils sub-circular, rimmed. Opening dorsal, nasal passage only slightly visible dorsally. Width of nostril/internarial distance = 0,19. Rostronasal distance/orbitonasal distance = 0,94. Minute pale pineal spot present. Extra-ocular proportion = 1,5. (See Van Dijk, 1966 for definitions of terminology). Spiracle single, sinistral, visible ventrally but not dorsally, situated 0,65 posteriorly along trunk. Opening slightly constricted, subcircular, visible laterally. Vent dextral, reaching margin of ventral fin.

Tail height subequal to trunk height. Tip rounded. Maximum height of fins occurs 0,2 posteriorly along tail. Tail length/length of head and trunk = 2,0. Height of caudal muscles at base of tail/height of trunk = 0,37.

Dorsal pigmentation uniform brown. Ventrally unpigmented except for slight stippling around the gut coils. Tail muscles slightly pigmented dorsally (Fig. 7). Fins unpigmented, except for slight markings on the dorsal fin.

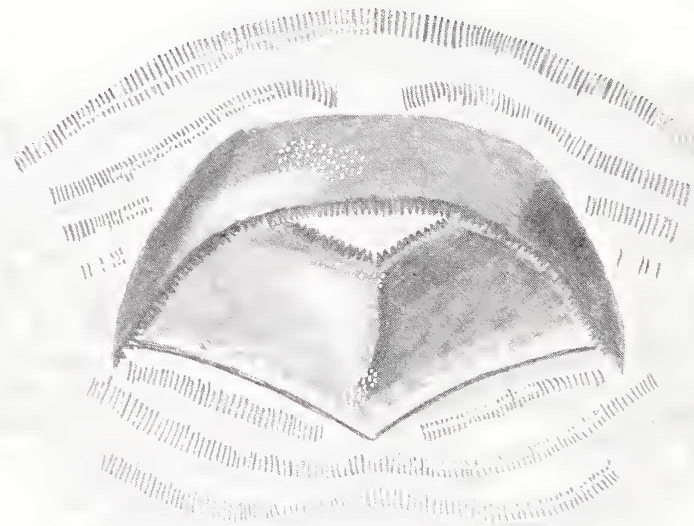

Fig. 6. Mouthparts of a tadpole of *Strongylopus springbokensis*.

Fig. 7. The tadpole of *Strongylopus springbokensis*.

DISCUSSION

The genus *Strongylopus* is believed to have had an origin in the high mountains of southern Africa (Channing, 1981). The Drakensberg massif has been suggested as a moist refuge during interpluvials (Brain and Meester, 1965). The mountains of Namaqualand and the south-western Cape could have served as speciation centres further south. *Heleophryne purcelli, H. regis, H. rosei, Capensibufo tradouwi, C. rosei, Breviceps montanus, Strongylopus bonaespei, S. springbokensis*, and *Arthroleptella lightfooti* are all endemic to the southern mountain ranges, supporting the hypothesis of a southern centre of speciation associated with high relief.

S. grayii and *S. springbokensis* are similar in appearance and presumably closely related. They can be easily separated on the basis of the advertisement call, the long call of *S. springbokensis* being very different from the single click of *S. grayii* (Channing, 1979). Preserved and other silent material can usually be separated morphologically on the sharper snout, wider head and shorter leg of *S. springbokensis*. These proportions can be combined as ratios of head width/tibia and foot/head width to give reliable diagnostic characters. The morphological similarity of the Wuppertal *S. grayii* to *S. springbokensis* remains a puzzle which probably will be solved by a phylogenetic analysis of the group.

The distribution of *S. springbokensis* will only be fully known when museum collections of material presently identified as *S. grayii* (or *Rana grayii*!) have been re-examined and the advertisement calls of the populations checked in the field. Further fieldwork is required to establish the geographical boundaries of the new species and the ecological interactions between it an other *Strongylopus* species, if any.

ACKNOWLEDGEMENTS

Mr Hannes Mostert kindly permitted access to his farm Bovlei where males were first found calling from oviposition sites. E. Baard and A. de Villiers lent material from the Cape Department of Nature Conservation collection. W. Haacke sent specimens of *S. grayii* from the Richtersveld for comparison and W. Branch collected material from Eksteenfontein. W. E. Duellman and J. Frost permitted the author to use a Sonagraph under their control while he was visiting the Museum of Natural History at the University of Kansas. All are thanked for their assistance. Bob Drewes is especially acknowledged for providing an opportunity to visit the type locality and for his enthusiastic help in the field.

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Editor
Dr F.W. GESS: 1978 –

Three new species of southern African *Bembix*, a new synonymy, and biological notes on other species of the genus (Hymenoptera: Sphecidae: Nyssoninae)

by

F.W. GESS

(Albany Musuem, Grahamstown)

CONTENTS

ABSTRACT

Three new species of southern African *Bembix*, *B. namibensis* **sp. nov.**, *B. zinni* **sp. nov.** and *B. karooensis* **sp. nov.** are described, *B. junodi* Arnold is sunk into synonymy with *B. ulula* Arnold, and biological notes are given for ten other species of *Bembix*. The nature of the prey of the genus *Bembix* with particular reference to Afrotropical species is reviewed and discussed.

INTRODUCTION

An investigation was made of the *Bembix* holdings of the major collections of southern Africa with a view to undertaking a taxonomic revision of the genus in that region. Three undescribed species and one synonymy were discovered. Some other taxonomic problems were identified but due to the inadequacy of the holdings of the relevant species and the consequent need for additional material from specific localities a taxonomic revision was considered to be premature. Consequently the new species and the synonymy only are dealt with in the present paper.

Over the years various biological observations on *Bembix* species have been gathered to-

gether. These are constituted from scattered published records, which in some instances are obscure and therefore generally overlooked, from specimen labels of Albany Museum material, and from personal observations. It is hoped that this represents as nearly as possible a complete compilation of the biological knowledge of *Bembix* in the Afrotropical Region and that it will as such form a foundation on which to build.

DESCRIPTIONS AND SYNONYMY

Bembix namibensis sp. nov.

MALE (Figs 1–8)

Black; mandibles excepting their apices, labrum, clypeus, face up to level of anterior ocellus (excepting for a pair of elongate wedge-shaped spots above antennal sockets), narrow bands widening below margining posterior orbits, scapes and flagella excepting broad dorsal black streaks, posterior margin and sides of pronotum, narrow streaks on mesonotum margining tegulae, anterior halves of tegulae themselves, bands margining scutellum and metanotum behind, anterior aspect of mesopleura and small marks on same behind pronotal lobes, mesosternum anteriorly and also along midline and adjacent to coxae, streaks on metapleura, markings of variable extent on sides of propodeum and including spiracular lobe, broad transverse bands on tergites 1–5, large central spot on tergite 6, visible part of gonostyles, sternites 1 and 2 at base and postero-laterial corners of sternites 1–5, legs (except black inner aspect of fore-femora and black streaks on foretibiae, inner aspect of femora and to a lesser extent of tibiae of middle and hind legs, comb on first tarsomere and distal extremities of all five tarsomeres of each fore-leg, claws and pulvilli of all legs), *various shades of yellow*.

Markings on tergites (except on lateral margins) almost white, markings on head pale yellow, those on thorax, legs, lateral margins of tergites and also the sternites darker yellow.

Extreme tip of tergite 7, centres of sternites 1 and 2 (and on the latter the raised projection), extreme margin of sternite 6 and whole of sternite 7, inner aspect of femora and to a lesser extent of tibiae of middle and hind legs, *light ferruginous*.

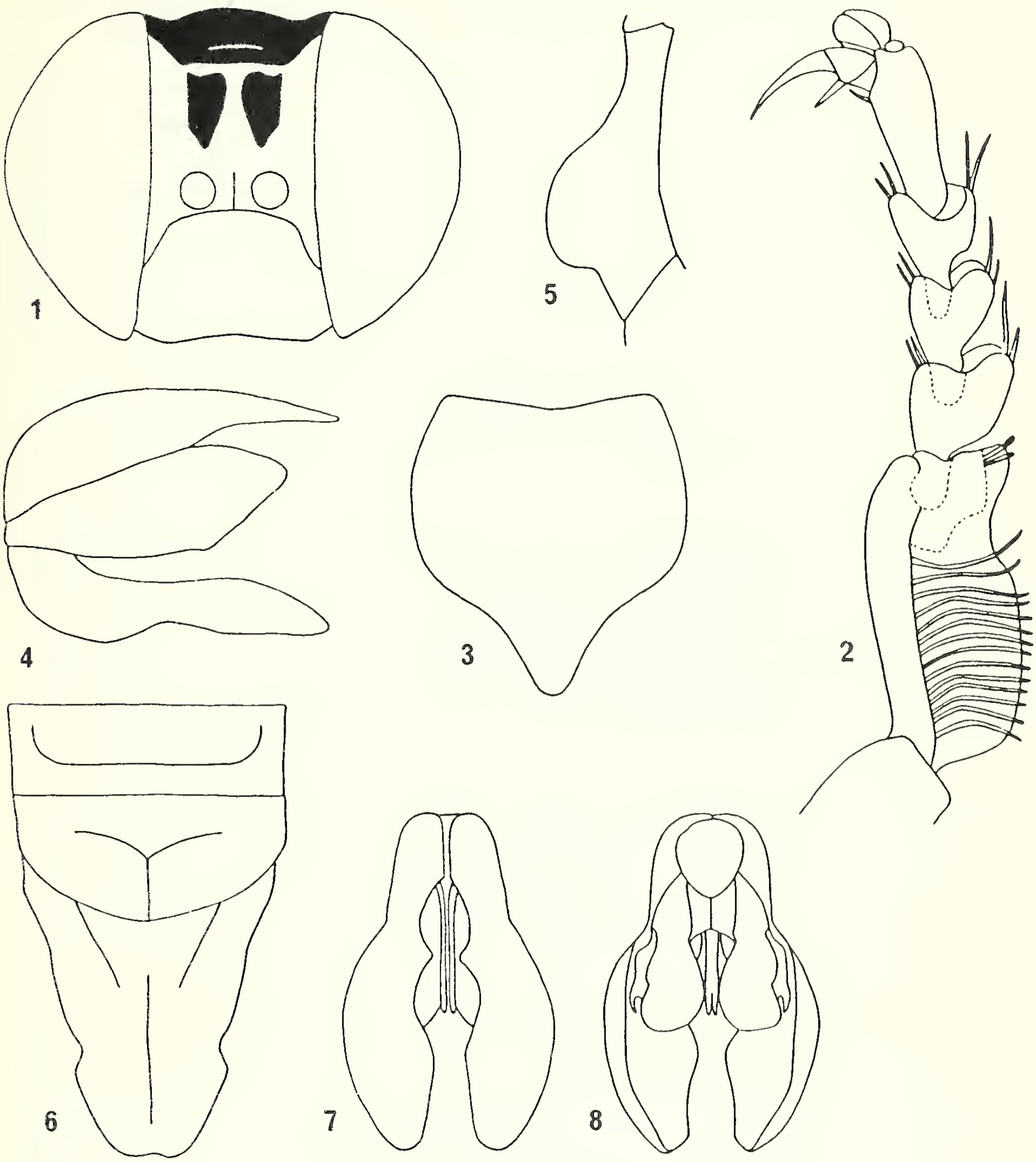
Wings absolutely clear; subcosta to junction with basal vein black, other veins brown (light brown proximally, darker brown distally).

Length of body 17–20 mm, length of wings 12–13 mm, hamuli 33–35.

Clypeus baso-laterally, face, occiput and back of head, thorax, propodeum, tergite 1 on declivous face and sternite 1 clothed with white pilosity, sparse everywhere except on mesopleura below and on mesosternum where dense; vestiture otherwise composed of short, decumbent, white pubescence, dense on clypeus and inner orbits below where shining, sparse elsewhere and apparently absent on propodeum above.

Puncturation generally fine and close; propodeum with somewhat coarser punctures; tergite 7 with large sparse punctures separated by wide shining interstices.

Mandibles lightly built, gracile, with the exception of a small tooth some way back from the apex tapering evenly to tip. Clypeus narrow, strongly convex; face narrow, at level of antennal sockets only very lightly wider than width of one eye, bluntly carinate below between antennal sockets (this carina carried over onto base of clypeus). Eyes slightly divergent below (Fig. 1). Scape robust, less than twice as long (excluding radicle) as maximum width. Flagellum with flagellomere 1 as long as 2, 3 and half of 4 together; flagellomeres 3–6 finely carinate be-



Figs 1–8. *Bembix namibensis* sp. nov. ♂: 1, head (frontal view); 2, right fore tarsus; 3, tergite 7 (dorsal view); 4, abdominal segment 7 (lateral view); 5, sternite 2 (lateral view, profile, anterior to top of figure); 6, sternites 5, 6 and 7 (ventral view); 7, genitalia (dorsal view); 8, genitalia (ventral view). (Figs 1, 3–8 are × 12; Fig. 2 is × 25).

low, 5 and 6 partially and 7–11 completely excavate below, 7–11 becoming progressively and strikingly larger (last flagellomere equal in length to pedicel and flagellomere 1 together).

Fore tarsi (Fig. 2) strikingly modified; first tarsomere greatly and evenly expanded laterally on one side into a thin, transparent lamella partially covered on the upper surface by fine concolourous pilosity and furnished apically beneath with an acutely pointed projection on the inner side and a pair of short flattened setae on the outer. Arising from the basic shaft of the first tarsomere but on its lower surface are two combs of greatly differing character: the first composed of 16 coarse, long, curved, parallel spines lies immediately beneath the lamella and in the same plane as the latter, the apices of the spines just exceeding the lateral margin of the lamella; the second comb composed of about an equal number (that is 16) of long, fine, curved hairs lies in a plane at right angles to the first. Tarsomeres 2, 3 and 4 also expanded but less so than 1; each (like 1) apically beneath with an acutely pointed projection on inner side and a pair of setae on the outer (these setae, however, longer, finer and not flattened).

Middle femora with posterior margin sharply angled, almost carinate, slightly undulate but not serrate nor anywhere toothed; middle tarsi modified.

Tergite 7 (Fig. 3) markedly narrowed over apical third, narrowly rounded apically, with lateral lobes (Fig. 4) broad (broadest at level where dorsal portion abruptly narrows) and coming to a point apically.

Sternite 2 (Fig. 5) with a large, raised, longitudinal, lamelliform projection on middle of disc, rising moderately steeply but smoothly anteriorly and falling in a smooth arc that is a quarter circle posteriorly. Sternites 4–7 modified (Fig. 6): 4 with a weak, hardly raised transverse line on middle of disc in posterior half; 5 with a posteriorly raised transverse platform over greater part of disc (margins of platform raised and carinate particularly at evenly rounded postero-lateral corners); 6 with a posteriorly raised very obtusely pointed triangular platform on centre of disc; 7 broadly rounded apically and with a single, weak, median carina.

Genitalia as figured (Figs 7 and 8).

Female unknown.

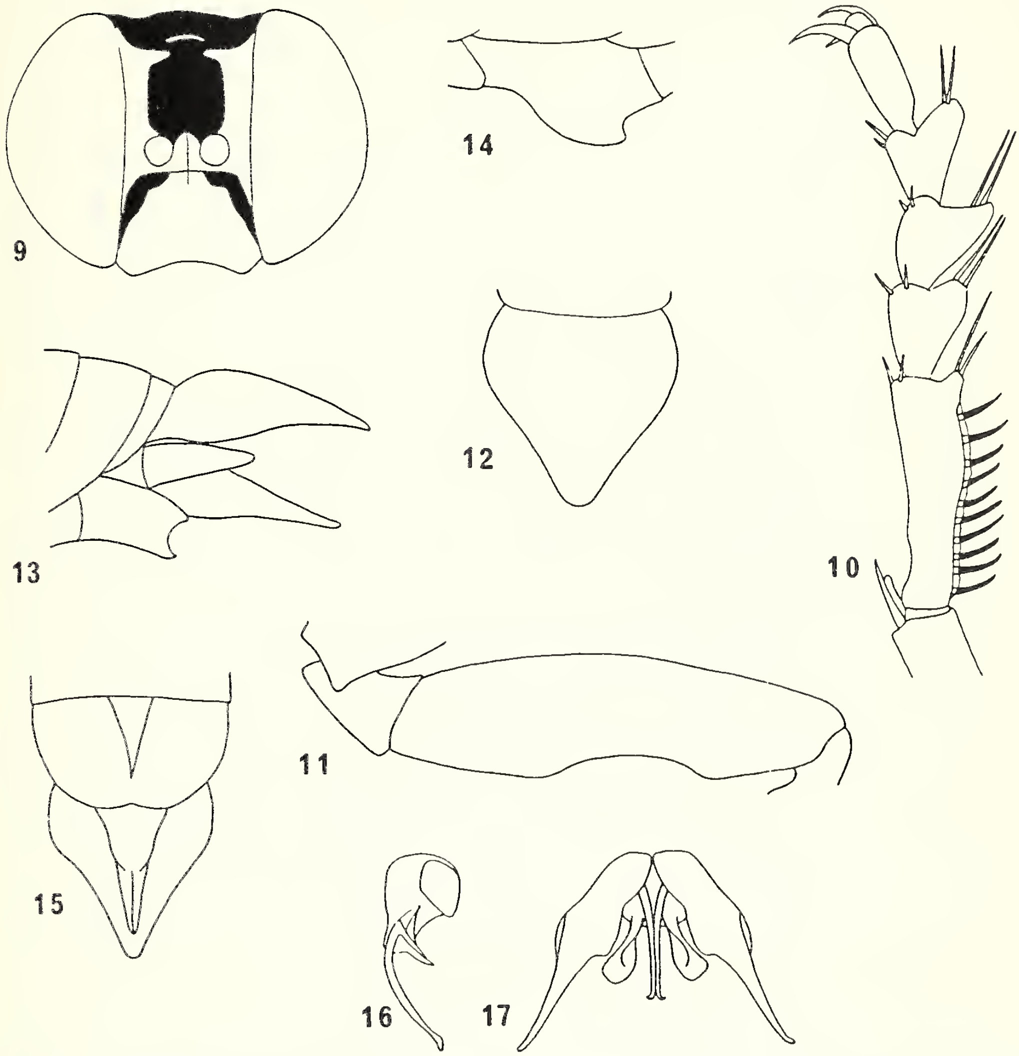
Material examined: South West Africa (Namibia): Namib Plain, 15 m. E Natab, 29.iv.1969 (H. D. Brown), Holotype ♂, Paratype ♂ (Albany Museum); Awasib Mains, Diamond Area No. 2, 14.v.1969 (H. D. Brown), Paratype ♂ (National Collection of Insects).

Etymology: The name, an adjective, is derived from the geographical name, Namib, and refers to the provenance of the described specimens.

Bembix zinni sp. nov.

Male (Figs 9–17)

Black; mandibles excepting their apices, labrum, clypeus (excepting for a pair of narrow triangular markings bordering sides and part of base (Fig. 9), face below and between antennal sockets, broad bands margining inner orbits to level of anterior ocellus, narrow bands widening below margining posterior orbits (but not meeting in the middle behind ocellar area as is the case in female), underside of scapes, posterior margin and sides of pronotum, narrow margins on mesonotum bordering tegulae, bands margining scutellum and metanotum behind, anterior aspect of mesopleura and backwardly curved vertical streaks on middle of same, most of metapleura, a pair of converging streaks on propodeum above and on declivity, sides of propodeum



Figs 9–17. *Bembix zinni* sp. nov. ♂: 9, head (frontal view); 10, right fore tarsus; 11, left hind femur; 12, tergite 7 (dorsal view); 13, end of abdomen (lateral view); 14, sternite 2 (lateral view, profile, anterior to left of figure); 15, sternites 6 and 7 (ventral view); 16, gonostyle (lateral view); 17, genitalia (dorsal view). (Figs 9, 11–17 are × 12; Fig. 10 is × 25).

(except posterior to spiracles) and posterior angles, transverse bands on tergites 1–4 or 5, entire tergite 6 (and sometimes 5), posterior half of tergite 7 (sometimes the entire exposed portion), sternite 1 (except for a pair of lateral spots), distal two-thirds of sternite 2, entire sternite 3, sides and posterior margin of sternite 4, posterior corners of sternite 5 and narrow lateral margins on sternite 6, legs (except for spots on coxae and trochanters, pulvilli), *light coloured*.

Markings on tergites 1–5 (except on lateral margins) almost *white*; markings on head and thoracic dorsum *pale yellow*; rest of thorax and abdomen as well as legs *darker yellow*; tergites 6 and 7 *orange yellow to light ferruginous*. Flagellum dark ferruginous above, lighter below, lanceolate spines on first tarsomere of each fore-leg *ferruginous*.

Wings absolutely clear; subcosta to junction with basal vein black, other veins brown (light brown proximally, darker brown distally).

Length of body 13–14 mm, length of wings 9 mm, hamuli 24–34.

Labrum, clypeus and inner orbits on lower half of face covered with a very fine, dense, decumbent, shining, silvery pubescence, most noticeable on clypeus; rest of head with fairly sparse, fine, white pilosity. Thorax and abdomen with fine, sparse, decumbent, white pubescence (not shining); thorax (especially pleura) and also propodeum with fine white pilosity (sparser than on head); last tergite margined by short, stout, light ferruginous bristles. Punctuation everywhere exceedingly fine and close except on last tergite which is furnished with large, sparse punctures separated by wide shining interstices.

Mandibles lightly built, with a small tooth some way back from the apex. Clypeus somewhat flattened in the middle in front (best seen in profile) but depressed area not as clearly delimited as in female. Inner margins of eyes parallel (Fig. 9). Face carinate below between antennae. Flagellum with flagellomere 1 about one-half longer than 2; flagellomeres 5–11 excavate below and therefore spined or laterally produced, each flagellomere up to and including the penultimate progressively more strongly excavate; ultimate flagellomere (11) markedly curved, almost angularly bent below.

Fore tarsi (Fig. 10) with first four tarsomeres dilated; first tarsomere with a row of about 10 short, stiff, flattened spines inserted below between midline of joint and margin.

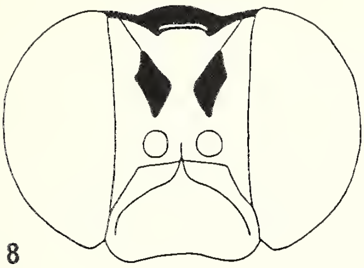
Middle femora finely serrate over most of the posterior margin; middle tarsi modified; hind femora shallowly but distinctly emarginate below (Fig. 11).

Tergite 7 and its lateral lobes as figured (Figs 12 and 13). Sternite 2 (Fig. 14) with a raised, arcuate, median longitudinal carina arising some distance from the anterior margin and ending some distance from the hind margin in a rounded slightly overhanging projection. Sternite 6 (Figs 13 and 15) with a narrow, acutely pointed, posteriorly raised triangular platform; sternite 7 narrow and apically pointed with a strong median and two feeble lateral carinae.

Genitalia (Figs 16 and 17) with gonostyles bifurcate; upper ramus long and narrow; lower ramus well sclerotised, untwisted, short and broad, rounded apically, situated below upper ramus and except for outside edges not visible from above.

Female (Figs 18 and 19)

Black; mandibles excepting their apices, labrum, clypeus, face (excepting for a pair of elongate spots above antennal sockets and a transverse band between eyes at level of ocelli), bands margining posterior orbits and meeting in the middle behind ocellar area, entire scape, flagellum (except for upper surface which narrowly brownish), posterior margin and sides of pronotum, wide lateral bands and a very well developed U-shaped mark on mesonotum, wide bands margining scutellum and metanotum, entire pleura and thoracic sternites, propodeum (except for a basal band margining metonatum and a narrow V-shaped band the point of which is on the declivity above the oriface and the arms of which end above the spiracles where they are downwardly produced), broad transverse bands on tergites 1–4 (that of tergite 1 containing a pair of oval black spots sometimes fused together and then either narrowly or broadly connected to basal black band, those of tergites 2 and 3 sometimes with small transverse black



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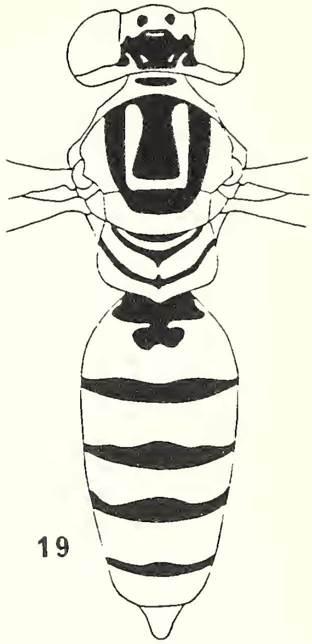

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Figs 18–19. *Bembix zinni* sp. nov. ♀: 18 head (frontal view); 19, head, thorax and abdomen (dorsal view). Fig. 18 is × 12; Fig. 19 is × 6)

spots), entire tergite 5, sternites 1–4 and distal two-thirds of 5, whole of legs (except small spot on hind coxae, pulvilli), *various shades of yellow*.

Tergite 6 and sometimes apex of sternite 5 *light ferruginous*.

Vestiture and puncturation very similar to that of male; shining silvery pubescence most noticeable on depressed region of clypeus.

Clypeus distinctly flattened in the middle in front with depressed area clearly delimited (Fig. 18). Other than for secondary sexual characters, very similar to the male.

Length of body 11,5–14 mm (Allotype 13,5 mm).

MATERIAL EXAMINED: Cape Province: Merweville Distr., Jan.–Feb. 1947 (H. Zinn) Holotype ♂, Allotype ♀, 2 Paratype ♂♂, 5 Paratype ♀♀; Merweville, Laingsburg Distr., i.1959 (H. Zinn), 2 Paratype ♀♀.

Holotype, Allotype, 1 Paratype ♂, 4 Paratype ♀♀ in South African Museum; 1 Paratype ♂, 3 Paratype ♀♀ in Albany Museum.

ETYMOLOGY: The name, in the genitive singular, is formed from the name of the collector of the present material. The author has pleasure in naming this species for the late Mr Humphrey Zinn, for 41 years on the technical staff of the South African Museum, whose enthusiastic collecting over the years, not only on official expeditions of which he was a member but also during his vacations, provided much valuable material so important for the study of our fauna.

***Bembix karooensis* sp. nov.**

MALE (Figs 20–24)

Black; mandibles excepting their apices, labrum, clypeus, face up to level of anterior ocellus (excepting for a pair of spots below ocellus), posterior orbits, scapes, pedicels, first flagellomeres below, posterior margin and lower half of sides of pronotum, pronotal tubercles (except for a central streak), prosternum bordering coxae, anterior portion of mesopleura and vertical bar below each tegula, mesosternum, two spots on metapleura below, spot of variable size on sides of propodeum and another anterior to each spiracle, legs (except for black markings on middle and hind coxae, streaks on upper side of femora and to a lesser extent of tibiae, lamellae of fore-tarsi and distal half on fifth tarsomeres and claws of all legs), most of sternites 1–3 and transverse posterior bands widening at sides on sternites 4 and 5, *lemon-yellow*.

Narrow band bordering sides and hind margin of scutellum, narrow apical band on metanotum, median transverse bands widening at sides on tergites 1–6 (those on 2–5 sometimes narrowly interrupted at midline and that on 6 sometimes not attaining lateral margins), *yellowish-white*.

Flagellomeres (with exception of first) light ferruginous below, dark above. Wings hyaline, veins light brown, subcosta as far as its junction with basal vein darker, almost black proximally.

Length of body 15–16,5 mm, length of wings 9–10 mm, hamuli 25–30.

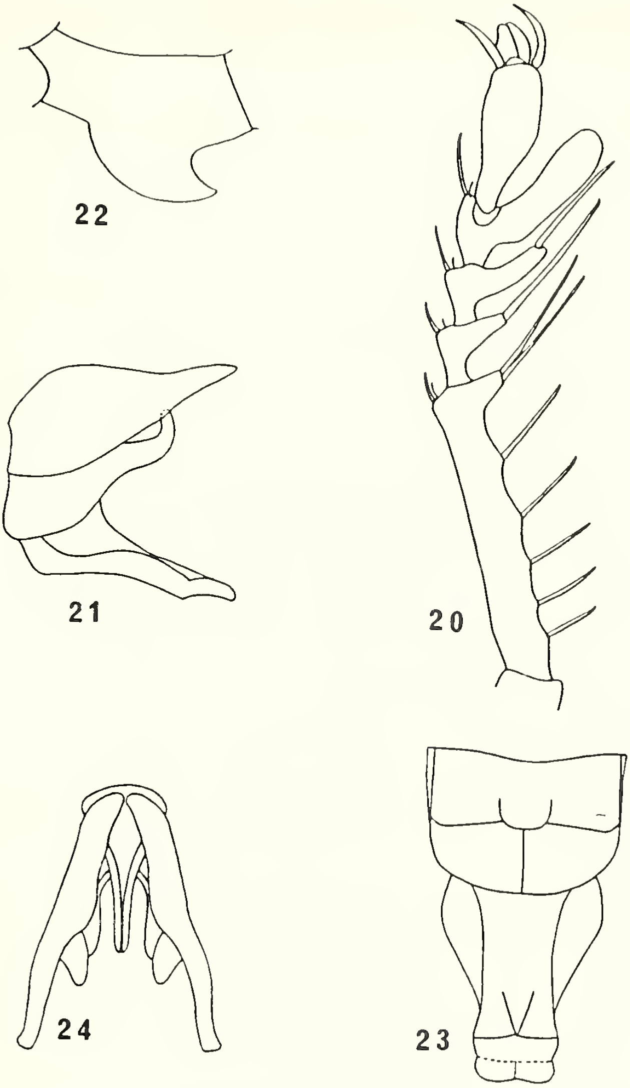
Labrum basolaterally, clypeus in greater part and inner orbits on lower half of face covered with a very fine, dense, decumbent, shining, silvery pubescence, most noticeable on clypeus; rest of head, entire thorax and propodeum and first abdominal segment with fine, long, erect, white pilosity; rest of abdomen with shorter, semi-erect, white pilosity; sixth tergite postero-laterally in addition with a number of dark, short, stout, apically-pointed setae. Puncturation everywhere very fine and close except on last tergite where somewhat larger and sparse with wide shining interstices.

Mandibles lightly built, with a small tooth some way back from the apex. Clypeus only slightly less than twice as wide as long, moderately but evenly convex. Inner margins of eyes parallel; face at level of antennal sockets 1,2 times wider than width of one eye, carinate below between antennal sockets. Scape robust, only twice as long (excluding radicle) as maximum width. Flagellum with flagellomere 1 as long as 2, 3 and half of 4 together; flagellomeres 5–11 modified, 5–7 each with a transverse ridge below near base (those on 6 and 7 spine-like in side view) and excavate below distal to ridges, 8–11 excavate below along their entire length.

Fore tarsi (Fig. 20) modified; first tarsomere weakly expanded laterally at insertion of spines, more strongly so distally; second to fourth tarsomeres progressively more strongly expanded laterally; third and fourth narrowly lamellate; fifth somewhat swollen.

Middle femora with fine serrations distally on posterior margin variously developed; middle tarsi modified.

Tergite 7 and its lateral lobes as figured (Fig. 21). Sternite 2 (Fig. 22) with a raised, arcuate and posteriorly pointed median longitudinal carnina; sternite 6 (Fig. 23) with a small, bluntly rounded, posteriorly raised platform about as wide as long; sternite 7 (Fig. 23) wide, lamelliform and truncate apically, swollen transversely subapically, with two parallel longitudinal carinae bounding sides and raised distally into triangular pointed lamellae bordering ends of transverse subapical swelling, with a triangular raised portion between parallel carinae and having its apex at middle of transverse swelling.



Figs 20–24. *Bembix karooensis* sp. nov. ♂: 20, right fore tarsus; 21, abdominal segment 7 (lateral view); 22, sternite 2 (lateral view, profile, anterior to left of figure); 23, sternites 6 and 7 (ventral view); 24, genitalia (dorsal view). Fig. 20 is × 25; Figs 21–24 are × 12).

Genitalia (Fig. 24) with gonostyles bifurcate; upper ramus long and more or less straight; the pair of upper rami subparallel; lower ramus weakly sclerotized, lamelliform.

Female

Black; mandibles excepting their apices, labrum, clypeus, face up to level of anterior ocellus (excepting for a pair of spots below ocellus), posterior orbits, scapes, pedicels, first flagellomeres below, posterior margin and whole of sides of pronotum, pronotal tubercles (except for narrow markings centrally), whole of prosternum, broad wedge-shaped markings bordering tegulae on each side of mesonotum and a pair of narrow longitudinal streaks on disc of same, bands on sides and posterior margins of scutellum and metanotum and band bordering disc of propodeum and extending some way down declivity medially, entire mesopleura, mesosternum and metapleura (except sutures), entire sides of propodeum (except small region behind spiracles), legs except for black streaks on upper sides of femora, the pulvilli and claws), broad median transverse bands widening abruptly laterally on tergites 1–5, large apical spot on tergite 6, entire sternites 1 and 2 and all but basal portion of sternites 3–5, *lemon yellow*.

Flagellum and wings coloured as in male. Vestiture and puncturation likewise similar to that of male.

Length of body 14–15 mm (Allotype 15 mm), length of wings 8,3 mm, hamuli 28–29.

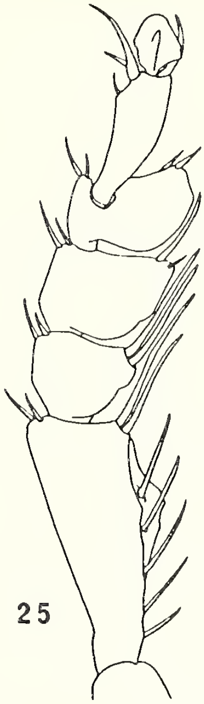
Material examined: Cape Province: Merweville, Laingsburg Distri., i.[19]59 (H. Zinn) Holotype ♂, Allotype ♀ (South African Museum); Merweville Distr., ii.1948 (H. Zinn) Paratype ♂ (South African Museum); Dikbome, Merweville, Koup, x.1952 (Mus. Exped.) 2 Paratype ♂♂ (Albany Museum). South West Africa (Namibia): 18 km from Ariamsvlei on road to Aroab, 14.v.1973 (C.F. Jacot-Guillarmod) Paratype ♀ (Albany Museum); Barby 26, Bethanie, SE2516DC, 2–7.x.1972 (no collector) (F9244) Paratype ♂ (State Museum, Windhoek).

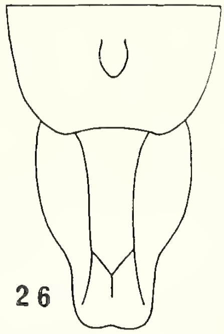
Etymology: The name, an adjective, is derived from the geographical name, Karoo, and refers to the provenance of the described specimens.

B. karooensis is allied to *B. cameronis* Handlirsch to which it bears a close superficial resemblance with respect to size, coloration and general facies. The following combination of characters is shared: in both sexes a wide face with parallel inner orbits; in the females short wings, and lateral carinae on tergite 6 enclosing a flattened pygideal area; in the males dilated fore-tarsomeres, postero-distally dentate middle femora, modified middle tarsomeres, a raised longitudinal carina on sternite 2, a raised platform on sternite 6, and two longitudinal carinae on a wide sternite 7.

The males may be distinguished by the form of the dilations of the fore-tarsomeres (in *cameronis* tarsomeres 1–4 are all more or less evenly expanded, the lamellate parts of 2, 3 and 4 being subquadrate) (Fig. 25), by the form of the raised platform on sternite 6 (in *cameronis* much smaller, narrower than long) (Fig. 26), by the details of the structure of sternite 7 (in *cameronis* the transverse subapical swelling and the lamelliform ends of the lateral carinae are absent) (Fig. 26), and by the form of the upper ramus of the bifurcate gonostyle (in *cameronis* wider and inwardly curved).

Females may be distinguished by means of the relative proportions of the scapes and of flagellomeres 1 and 2. In *karooensis* the length of flagellomere 1 is twice that of flagellomere 2 and the combined length of these two flagellomeres exceeds the length of the scape (without radicle) by a factor of almost 1,2. In *cameronis*, on the other hand, the length of flagellomere 1 is less than twice that of flagellomere 2 and the combined length of these two flagellomeres equals that of the scape (without radicle).





Figs 25–26. *Bembix cameronis* Handlirsch ♂: 25, right fore tarsus; 26, sternites 6 and 7 (ventral view). (Fig. 25 is × 25; Fig. 26 is × 12).

Bembix ulula Arnold and *Bembix junodi* Arnold

Bembex ulula Arnold, 1929: 330, figs 2, 2a, 2b, Pl. VI, figs 3 and 43, ♂, ♀; Arnold, 1935: 503.
Bembex Junodi Arnold, 1929: 379, figs 42, 42a, 42b, 42c, Pl. VI, fig. 45, ♂, **syn. nov.**

Bembix ulula Arnold was described from four localities in Rhodesia (now Zimbabwe): Victoria Falls, Gwaai, Sawmills and Springvale. An additional specimen was recorded by Arnold (1935) from Kuke Pan, Kalahari (in Botswana).

Bembix junodi Arnold, described from Lourenço Marques (now Maputo) in Moçambique, is known only from the type material (2♂♂) in the Transvaal Museum.

According to the descriptions and also Arnold's key to species, the outstanding difference between the males of the two species is to be found in the structure of the genitalia, which indeed look very different in the figures (2b and 42c). Examination, however, of the two specimens of *junodi* showed that the gonostyles (Arnold's "outer paramera") of the holotype (which had the genitalia extracted but still attached) were damaged distally, whereas what little could be seen of the tips of these structures in the paratype suggested that they were quite different from the figure (42c) but similar to the bifurcate gonostyles of *ulula*. Subsequent partial extraction of the genitalia of the paratype confirmed that that specimen could indeed be as-

signed to *ulula*, as could also the holotype which differs from the paratype only with respect to the state of repair of the gonostyles. It appears that the gonostyles of the holotype were damaged already at the time of description and that the figure (42c), as indeed the species *junodi*, is based upon these broken gonostyles the missing apices of which were incorrectly "reconstructed" in the drawing.

It is significant that of all the species seen by Arnold (1929) *junodi* was the only one which he was unable to assign to any of Handlirsch's species groups; furthermore, that, despite this, *junodi* and *ulula* run down together to the same couplet in his key. The differences given by Arnold for the relative proportions of the flagellomeres in the two species are illusory.

Bembix ulula Arnold has position precedence and *B. junodi* Arnold must therefore sink into synonymy.

MATERIAL EXAMINED: Cape Province: Kalahari Gemsbok Park, Nossob Camp, 24–27.iv.1973 (M. W. Mansell) (Malaise trap) ♀ (Albany Museum). Natal: Manguzi River nr. Maputa, Z[ululand], xi–xii–1945 (H. Bell Marley) ♂ (Albany Museum). Rhodesia (now Zimbabwe): Gwaai, 16.i.1927 (G. Arnold) Holotype ♂ of *B. ulula*, 2♀♀ (South African Museum ex National Museum Bulawayo 1981); Gwaai, 16.i.1927 (Rhodesia Museum) Allotype ♀ of *B. ulula* (South African Museum ex National Museum Bulawayo 1981); Insuza River, 24.xii.1939 (Nat. Museum of S. Rhodesia) ♂ (South African Museum ex National Museum Bulawayo 1981); Lupane, xii.1938 (National Museum of Rhodesia) ♂ (South African Museum ex National Museum Bulawayo 1981); Lupane, xii.1938 (National Museum of Rhodesia) ♀ (Albany Museum); Sawmills, 22–27.xii.1923 (R. H. R. Stevenson) ♀ (Albany Museum); Sawmills, 22.ii.1925 (Rhod. Museum) ♀ (South African Museum ex National Museum Bulawayo 1981); Sawmills, 4.ii.1926 (R. H. R. Stevenson) ♀ (South African Museum ex National Museum Bulawayo 1981); W. Matetsi, iv.1934 (R. H. R. Stevenson) 2♀♀ (South African Museum ex National Museum Bulawayo 1981). Moçambique: Lour[enco] Marques, Jan. (no year) (Rev H. A. Junod) Holotype ♂ of *B. junodi* (Type No. H–193) (Transvaal Museum); Lour[enco] Marques, (no date) (Rev H. A. Junod) Paratype ♂ of *B. junodi* (Paratype No H–194) (Transvaal Museum).

BIOLOGICAL NOTES

Nesting observations were made during the course of a survey of the aculeate wasps of a karroid area to the WNW of Grahamstown (33° 19′ S, 26° 32′ E) in the Eastern Cape Province. Nesting sites of *B. albofasciata* Smith, *B. cameronis* Handlirsch, *B. melanopa* Handlirsch and *B. sibilans* Handlirsch were located on the farm Hilton, 18 km WNW of Grahamstown. An additional nesting site of *B. albofasciata* and *B. sibilans* was located on the farm Slaaikraal, 9 km WNW of Grahamstown. A detailed account of various aspects of the ecology of Hilton has been given previously (Gess, 1981: 3–9). The nesting substrate in both localities is light-coloured, fine-grained sand derived from the weathering of Witteberg quartzite. In addition some observations of two littoral species, *B. arnoldi* Arnold and *B. fraudulenta* Arnold, were made at Boknes, 47 km S of Grahamstown, and at Riet River Mouth, 57 km ESE of Grahamstown. The beaches at these two localities are relatively wide, sandy and backed by low dunes colonized by pioneer plants. All species were represented by a few individuals only.

In addition prey records, pertaining to these and to other species, derived from specimens in the Albany Museum are included.

Biological observations, unless otherwise attributed, are jointly those of the author, S. K. Gess and D. W. Gess with the very able assistance of H. W. Gess and R. W. Gess. All the prey listed were determined by the author and either constitute previously unpublished records or amplifications of those published in Gess (1981).

***Bembix albofasciata* Smith**

Nesting sites

At Hilton *B. albofasciata* nests in loose sand on a gently sloping roadside bank and in horizontal to gently sloping loose sand outside the rim of a sandpit dug in an alluvial deposit of sand deposited on the floodplain of a seasonal tributary of the New Year's River. At Slaaikraal the nesting site is similarly on the fringe of a sandpit, in this locality, situated at the foot of a hill slope in the rain shadow.

Flight period

Males and females were collected in the vicinity of the nesting sites from late November to late February and nesting was recorded from early December to late February.

Plants visited by adult wasps

No observations were made of plant visiting at Hilton or Slaaikraal, however, two males and 21 females were collected on flowering *Foeniculum vulgare* Mill. (Umbelliferae) and two females on flowering lucerne in Belmont Valley which extends SE from Grahamstown.

Description of the nest (Fig. 27)

Fourteen nests were excavated. All were single-celled. The nest consists of a short trench leading to a subcircular entrance hole from which extends a burrow, shallow at first and then

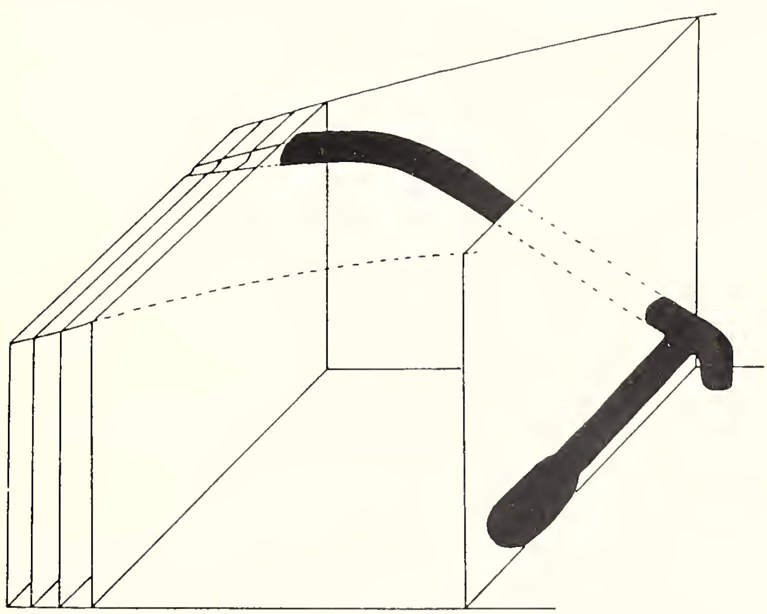


Fig. 27. *Bembix albofasciata* Smith: Plan of nest C from Hilton, 10.i.1975.(× 0,5)

turning downwards more steeply to reach an average depth of 95 mm (range 75–135 mm; sample 13) at which level there is most typically a change in direction of from 45–90°. The burrow terminates in a cell at an average distance of 56 mm (range 42–73 mm; sample 8) from the angle. The diameter of the main burrow is an average of 9 mm (range 7–10 mm; sample 14) and of the cell an average of 14 mm (range 13–18 mm; sample 9). In six of the 14 nests excavated there was a distinct spur at the change in direction of the burrow. The spur continued in the same direction as the initial shaft but was directed sharply downwards.

Method of construction of the nest and provisioning

Like its congeners, *B. albofasciata* is a 'raker'. In digging the fore-tarsi are bent towards the mid-line of the body and are moved repeatedly backwards and forwards, each back stroke throwing back a load of sand which passes beneath the upheld abdomen to behind the body. There was no evidence of sand being raked away from the burrow entrance, in fact the burrow is characterized by the presence of a tumulus of excavated sand at the outer end of the entrance trench.

Provisioning is progressive. During the period of provisioning a temporary closure is maintained whilst the female is away from the nest and the approach to the cell is kept loosely filled with sand.

Prey

Nest A: Hilton, 8.xii.1974.		
Tabanidae	*Chrysops obliquefasciatus* Macq.	1♂
Asilidae	?*Xenomyza* sp.	1♂
Muscidae	*Musca lusoria* Weid.	1♂
Nest B. Hilton, 8.xii.1974		
Stratiomyidae	?Genus and species	1♂
Asilidae	*Synolcus* sp.	1♀
Conopidae	?Genus and species	1
Calliphoridae	?Genus and species	3
Nest C: Hilton, 10.i.1975		
Stratiomyidae	?Genus and species	1♂
Mydidae	*Nomoneura caffra* Hesse	1♀
Asilidae	*Synolcus* sp.	1♀
	Stenopogon dilutus (Walker)	1♀
	?Genus and species	1
Sarcophagidae	*Sarcophaga* sp.	2
Nest D (77/78/141): Hilton, 2.i.1978		
Stratiomyidae	?Genus and species	1♂
Calliphoridae	*Chrysomya ?putoria* (Wied.)	1
Nest E (77/78/205): Hilton, 18.i.1978		
Tachinidae	?Genus and species	1
Nest F (77/78/224): Hilton, 7.ii.1978		
Bombyliidae	*Lomatia pictipennis* (Wied.)	1
Calliphoridae	?Genus and species	1

Nest G (82/83/62): Slaaikraal, 2.xii.1982		
Bombyliidae	*Exoprosopa* sp.	1
Nest H (82/83/102): Hilton, 9.xii.1982		
Asilidae	?Genus and species (*Neolophonotus* group)	1♂
Bombyliidae	*Geron* sp.	1♂
	?*Geron* sp.	1♀
Muscidae	*Musca* sp.	3♂♂(+2?)
Calliphoridae	?Genus and species	3♀♀, 4♂♂(+2?)
	?Genus and species	1♀
Tachinidae	?Genus and species	1♀, 1♂
Nest I (82/83/104): Hilton, 9.xii.1982		
Asilidae	*Synolcus* sp.	1♂
	Acnephalum andrenoides (Wied.)	1♂
Bombyliidae	*Systoechus* sp.	2♂♂, 1♀, 1
	Henica longirostris (Wied.)	1♀
	Exoprosopa sp.	1
	Villa ?*vitripennis* (Loew)	3
Calliphoridae	?Genus and species	2 (+?)
Tachinidae	?Genus and species	1 (+?)

Females captured at nest entrance with prey:

Hilton, 8.xii.1974, Calliphoridae, ?genus and species, ♂; Hilton, 10.i.1978, Bombyliidae, *Exoprosopa* sp., 1; Hilton, 9.ii.1978, Bombyliidae, *Lomatia pulchriceps* Loew, ♂; Hilton, 9.ii.1978, Bombyliidae, *Lomatia pictipennis* (Wied.), ♂; Hilton, 21.ii.1983 Calliphoridae, ?genus and species, ♀.

Additional records derived from specimens in the Albany Museum:

Lesotho, Mamathes, 18.xii.1949 (C. Jacot-Guillarmod), Tachinidae, ?genus and species, ♀; Lesotho, Mamathes, 26.ii.1944 (C. Jacot-Guillarmod), Asilidae, *Neolaparus* sp., ♀; Lesotho, Mamathes, 14.ii.1950 (C. Jacot-Guillarmod), Syrphidae, *Eristalis tenax* (L.), ♀; O.F.S., Chicago, Lindley Dist., 17–28.i.1968 (D. J. Brothers), Calliphoridae, *Chrysomya marginalis* Wied., ♂; O.F.S., Chicago, Lindley Dist., 17–28.i.1968 (D. J. Brothers), Sarcophagidae, *Sarcophaga* sp., 1.

Bembix arnoldi Arnold

Plants visited by adult wasps

Males and females of *B. arnoldi* were collected in January, 1984 on flowers of *Hydrophylax carnosa* (Hochst.) Sond. (Rubiaceae) growing on low fore-dunes at Boknes.

Nesting

No provisioned nests have been found, however, individuals have been observed digging burrows in level sand on the seaward side of the fore-dunes at Boknes. Whether these were for nesting or for sheltering is not known.

Hunting and prey capture

Some observations were made by D. W. Gess on hunting and prey capture by *B. arnoldi* at Boknes on 25.i.1984. Scattered piles of ocean wrack are deposited along the tide line. Those which have been exposed for some hours are attended by large numbers of small flies. A female *B. arnoldi* was observed flying low over the seaweed and patrolling a distance of about 10 m. Every now and then she came to rest on the sand for a few seconds which she spent grooming. On one occasion the wasp swooped down and picked up a small piece of debris, apparently mistakenly as it was dropped. Eventually a small fly was captured. The wasp swooped down, grabbed the fly and stung it in mid-air whilst hovering about 15 cm above the ground. The wasp reached underneath the fly with its abdomen and stung it from below. Once stinging had been completed the wasp prepared to fly away but was captured.

The prey was a small muscid. *Adersia oestroides* Karsch (Tabanidae) was commonly present in the vicinity of the wrack but was ignored by *B. arnoldi*.

***Bembix cameronis* Handlirsch**

Nesting site

At Hilton a nest of *B. cameronis* was found within the sandpit in the level floor of the pit.

Flight period

At Hilton males have been collected from early November to early December and females from early December to early January. The single nest was excavated in mid-December and a female was captured with prey in January.

Plants visited by adult wasps

At Hilton males and females have been collected visiting flowers of Compositae—*Senecio* sp. (4♀♀ and 3♂♂), *Athanasia* sp. (♂), *Lasiospermum bipinnatum* (Th.) Druce (♀).

Description of the nest

The single nest consisted of an evenly sloping burrow 7 mm in diameter ending in a horizontally aligned cell at a depth of 90 mm. The diameter of the cell was 11 mm. The total length of the burrow including the cell was 210 mm. There was no indication of a lateral branch or of a spur.

Prey

Female captured with prey:

Hilton, 10.i.1984, Bombyliidae, *Systoechus* sp., ♀.

Additional record derived from specimen in the Albany Museum:

Lesotho, Bokong P.O., 26.xii.1946 (A. Jacot-Guillarmod), Bombyliidae, *Systoechus* sp., ♂.

***Bembix capensis* Lepeletier**

Prey

Female captured with prey:

Hilton, 2.xii.1977, Tachinidae, ?genus and species, 1.

Additional record derived from specimen in the Albany Museum:

Transvaal, Pretoria North sandpits, 25.10.1947 (C. Jacot-Guillarmod), Sarcophagidae, *Sarcophaga* sp., ♀.

***Bembix capicola* Handlirsch**

Prey

Records derived from specimens in the Albany Museum:

Lesotho, Mamathes, i.1940 (C. Jacot-Guillarmod), Syrphidae, ?genus and species, ♂; Lesotho, Mamathes, i.1940 (C. Jacot-Guillarmod), Tachinidae, ?genus and species, ♀; Lesotho, Mamathes, i.1940 (C. Jacot-Guillarmod), Calliphoridae, ?genus and species, ♂.

Record derived from specimen in the South African Museum:

Lesotho, Mamathes, i.1940 (C. Jacot-Gullarmod), Muscidae, ?genus and species, 1.

***Bembix flavocincta* Turner**

Prey

Records derived from specimens in the Albany Museum:

Malawi, Domira Bay, Lake Nyassa (alt.1760), no date, (J. B. Casey), Bombyliidae, ?genus and species, ♀; Malawi, Domira Bay, Lake Nyassa (alt.1760), no date, (J. B. Casey), Sarcophagidae, *Sarcophaga* sp., ♀.

***Bembix fraudulenta* Arnold**

Plants visited by adult wasps

Males and females were collected on flowers of *Hydrophylax carnosa* (Hochst.) Sond. (Rubiaceae) growing on low fore-dunes at Boknes (13♂♂ and 5♀♀), of *Ipomoea brasiliensis* (L.) Sweet (Convolvulaceae) growing on low fore-dunes at Riet River Mouth (4♂♂), of *Gazania* sp. (Compositae) growing on fore-dunes at Boknes (♀), and of a white-flowered "mesem" (Mesembrianthemaceae) at Kenton-on-Sea (45 km SSE of Grahamstown) (♀).

Prey

Record derived from specimen in the Albany Museum:

Natal, Umhlanga Rocks, 1.i.1955 (E. McC.Callan), Mydidae, *Nomoneuroides natalensis* Hesse (♂).

***Bembix melanopa* Handlirsch**

Nesting sites

At Hilton *B. melanopa* nests in the sloping banks of the sandpit.

Flight period

Males and females were collected at Hilton from mid-November to mid-February and nesting was recorded in mid-November and mid-January.

Plants visited by adult wasps

No observations were made of plant visiting at Hilton, however, two females were collected on flowering *Foeniculum vulgare* Mill. (Umbelliferae) 5 km N of Alexandria on the road to Salem.

Description of the nest

Three nests were excavated. Two were single-celled and the third had not reached the stage of cell construction. The nest burrows, 9 mm in diameter, sloped evenly downwards for a

distance of 215 and 240 mm before changing in direction and after a further 20 mm terminated in an upwardly directed cell greater in diameter than the shaft. In one of the nests a spur was present shortly before the change in direction of the burrow.

Method of construction of the nest

Whether or not a tumulus accumulated below the nest entrance was dependant upon the steepness of the slope in which the nest was excavated. Sand was not raked away from the entrance.

By comparison the method of excavation of a sheltering burrow observed at Boknes is of interest. The burrow was excavated in sloping sand below a carpark. Digging was performed in the manner described for *B. albofasciata*, however, no tumulus was allowed to develop, the excavated sand being frequently raked away. After a time sand was no longer removed from the burrow but allowed to accumulate just within the mouth of the burrow until it was completely occluded and concealed.

Prey

Nest J (82/83/12): Hilton, 16.xi.1982.

Muscidae	*Musca* sp.	4
Calliphoridae	?Genus and species	1♂
Sarcophagidae	*Sarcophaga* sp.	1
Tachinidae	?Genus and species	1

Nest K (83/84/72): Hilton, 10.i.1984.

Syrphidae	*Eristalinus taeniops* (Wied.)	2♀♀, 4♂♂
	?Genus and species	1♀, 1♂
Calliphoridae	?Genus and species	3♀♀ (+1?)
	?Genus and species	1?

Additional records derived from specimens in the Albany Museum:

Cape Province, Fort Beaufort, 20.i.1960 (C. Jacot-Guillarmod), Muscidae, *Musca* sp., ♂; Cape Province, Natures Valley, 28.xii.1966 (A. Jacot-Guillarmod), Tabanidae, *Philoliche (Phara) flavipes* Macq., ♀.

***Bembix moebii* Handlirsch**

Record derived from specimen in the Albany Musuem:

Transvaal, Sewefontein, 15 miles E of Middelburg, 5.xii.1973 (A. L. Dyce), "Observed catching tabanids feeding on cattle".

***Bembix sibilans* Handlirsch**

Nesting sites

B. sibilans was found nesting in relatively horizontal ground at Hilton and on the side of a sandpit at Slaaikraal.

Flight period

At Hilton males were collected from November to February and females from December to March. Nesting was recorded in early December at both Hilton and Slaaikraal.

Plants visited by adult wasps

At Hilton females were captured visiting flowers of *Phyllopodium cuneifolium* Benth. (Scrophulariaceae) (1♀) and *Anchusa capensis* Th. (Boraginaceae) (1♀).

Description of the nest

Two nests were excavated. Both were single-celled. Both consisted of an evenly sloping burrow 8 mm in diameter ending in a cell. In the nest in the sloping bank the cell was in the same plane as the shaft and in the nest in level ground the cell was positioned horizontally. In both instances the diameter of the cell was 14 mm. The lengths of the shafts were 80 and 130 mm respectively. There was no indication of a spur in either nest.

Prey

Nest L (82/83/63) Slaaikraal, 2.xii.1984.

Tabanidae	*Amanella minor* Oldroyd	1♂
Bombyliidae	*Lomatia oreoica* Hesse	1♂
	Exoprosopa sp. A	17
	Exoprosopa sp. B	3
	Exoprosopa sp. C	1

Nest M (82/83/70) Hilton, 3.xii.1982.

Nemestrinidae	*Atriadops vespertilio* (Loew)	4♂♂
Bombyliidae	*Bombylius delicatus* Wied.	1♀
	?*Systoechus* sp.	2
	Exoprosopa sp.	4
	Villa vitripennis (Loew)	1
	?Genus and species	1
	?Genus and species	1
	?Genus and species	1
Calliphoridae	?Genus and species	2
	?Genus and species	3
Sarcophagidae	*Sarcophaga* sp.	1
Tachinidae	?Genus and species	1♀

Additional record derived from specimen in the Albany Museum:

Transvaal, Mooiplaas, Spekboom River, 30 miles N of Lydenburg, 26.xi.1973 (A. L. Dyce), "observed catching tabanids".

REVIEW OF THE NATURE OF THE PREY OF THE GENUS BEMBIX WITH PARTICULAR REFERENCE TO AFROTROPICAL SPECIES

The genus *Bembix* is a modern genus of nearly world wide distribution. Knowledge of the ethology of the genus was until recently limited very largely to that of species occurring in the northern hemisphere. These species, at least all of those studied, prey exclusively upon Diptera. A few fragmentary and in some instances not very well authenticated records of some southern hemisphere species hunting non-dipterous prey were consequently treated with considerable caution.

This situation has in recent years been strikingly modified. Following approximately twelve months of field work in Australia, Evans and Matthews (1973 and 1975) showed that the Australian *Bembix* exhibit unusual radiation with respect to prey. Of the 22 species studied in the field about one-third were found to prey upon insects of orders other than Diptera. Three species took only bees (chiefly social, stingless bees of the genus *Trigona*), one species took only wasps (Thynninae), one took only ant lions (Neuroptera) and one only damselflies (Odonata). Two species in transition with respect to prey preference took both flies and other insects, one bees and wasps and the other damselflies.

The exciting findings with respect to the Australian fauna show that, whereas it remains true that the vast majority of *Bembix* species prey upon Diptera, it would be wrong simply to assume that any given species of unknown ethology preys upon flies. It is therefore not only valid but necessary to record the prey preference of each and every species for even if the preference is only for flies it will at least have been established with certainty that it is not for any other group. It seems that this approach is particularly appropriate with respect to the Afrotropical species which, despite their large number (Bohart and Menke, 1976, list about 90) are poorly known ethologically and may consequently provide some surprises though most probably not upon the Australian scale.

One or possibly two Afrotropical species have indeed been found to use not Diptera but adult Lepidoptera as prey. Carpenter (1917) recorded observing an unidentified *Bembix* species hunting and capturing an hesperiid butterfly near Tabora in central Tanganyika (now Tanzania). Of greater value are the observations of Stevenson in Southern Rhodesia (now Zimbabwe) reported by Benson (1934). These concerned *Bembix regnata* Parker (= *B. speciosa* Arnold) which was recorded as regularly catching butterflies, "usually species of *Terias* (Pieridae) and small Hesperiidae, but sometimes Nymphalidae, for example once *Charaxes etheocles* Cram., ♂, and once *Pyrameis cardui* L., and also once a Hesperid of middle-size, *Abantis zambesiaca* Westw.". Some of Stevenson's material (*Bembix* ♀♀ and prey), exhibited on 3 October 1934 at a meeting of the Royal Entomological Society of London, is in the collection of the British Museum (Natural History) and was examined there by the present author in 1984. Label data, not given by Benson (1934) are: Westwood near Matetsi, Southern Rhodesia, 30.3.19[34], R. H. R. Stevenson.

Information regarding the prey of twelve (possibly thirteen) Afrotropical *Bembix* species has been published (Benson, 1934; Bequaert, 1932; Carpenter, 1917 and 1920; Cuthbertson, 1933 and 1939; Gess, 1981; Ullyett and De Vries, 1940). Prey records for a further six species are presented in the present paper as are additional records pertaining to four species for which prey is already known. All available records pertaining to the total of 18 (possibly 19) species are indicated in Table 1, the prey being identified to family only.

The subject of prey selection by *Bembix* species has been dealt with by Evans (1957: 11–12, 211; 1966: 357). The present information pertaining to the Afrotropical species, both that presented here as new and that given by other authors (see Table 1), is in accord with Evans' generalizations based upon the Diptera-hunting North American and Eurasian species.

All the species for which fair numbers of prey species have been collected and for which it is consequently possible to form an assessment show little selection as to the type of fly utilized. Prey belonging to a wide range of families is taken (Table 1), the qualifying criterion apparently being one of size. No Nematocera have been recorded as prey. Among the Brachycera, the Tabanidae and Bombyliidae are most often represented whereas, among the Cyclor-

Table 1.

Prey (identified to family only) of Afrotropical species of *Bembix*.

Bembix species	Prey		Reference
B. albofasciata Smith	DIPTERA	Stratiomyidae Tabanidae Mydidae Asilidae Bombyliidae Syrphidae Conopidae Muscidae Calliphoridae Sarcophagidae Tachinidae	Gess (1981); Present paper Gess (1981); Present paper Present paper Gess (1981); Present paper Gess (1981); Present paper Present paper Gess (1981); Present paper Gess (1981); Present paper Gess (1981); Present paper Present paper Gess (1981); Present paper
B. arnoldi Arnold	DIPTERA	Muscidae	Present paper
B. bequaerti dira Arnold	DIPTERA	Tabanidae unspecified*	Bequaert (1932) Bequaert (1932)
B. braunsii Handlirsch	DIPTERA	Tabanidae unspecified*	Bequaert (1932) Bequaert (1932)
B. cameronis Handlirsch	DIPTERA	Bombyliidae	Present paper
B. capensis Lepeletier	DIPTERA	Tabanidae Glossinidae Calliphoridae Sarcophagidae Tachinidae unspecified	Carpenter (1920) Carpenter (1920) Ullyett & De Vries (1940) Present paper Gess (1981); Present paper Carpenter (1920); Ullyett & De Vries (1940)
B. capicola Handlirsch	DIPTERA	Syrphidae Muscidae Calliphoridae Tachinidae unspecified	Present paper Present paper Ullyett & De Vries (1940): Present paper Present paper Ullyett & De Vries (1940)
B. flavocincta Turner	DIPTERA	Bombyliidae Sarcophagidae	Present paper Present paper
B. forcipata Handlirsch	DIPTERA	Glossinidae unspecified	Carpenter (1920) Carpenter (1920)
B. fraudulenta Arnold	DIPTERA	Mydidae	Present paper

Bembix species	Prey		Reference
B. fuscipennis Lepeletier	DIPTERA	Tabanidae Bombyliidae Syrphidae Muscidae Calliphoridae Sarcophagidae Tachinidae	Cuthbertson (1939) Cuthbertson (1939) Cuthbertson (1939) Cuthbertson (1939) Cuthbertson (1939) Cuthbertson (1939) Cuthbertson (1939)
B. massaica Cameron	DIPTERA	Calliphoridae	Cuthbertson (1933)
B. melanopa Handlirsch	DIPTERA	Tabanidae Bombyliidae Syrphidae Muscidae Calliphoridae Sarcophagidae Tachinidae unspecified	Cuthbertson (1939); Present paper Cuthbertson (1939) Cuthbertson (1939); Present paper Cuthbertson (1939); Gess (1981); Present paper Cuthbertson (1939); Ullyett & De Vries (1940); Present paper Cuthbertson (1939); Present paper Cuthbertson (1939); Present paper Ullyett & De Vries (1940)
B. moebii Handlirsch	DIPTERA	Tabanidae	Present paper
B. olivata Dahlbom	DIPTERA	Calliphoridae unspecified	Ullyett & De Vries (1940) Ullyett & De Vries (1940)
B. sp. (?*regnata* Parker)	LEPIDOPTERA	Hesperiidae	Carpenter (1917)
B. regnata Parker	LEPIDOPTERA	Pieridae Hesperiidae Nymphalidae	Benson (1934) Benson (1934) Benson (1934)
B. sibilans Handlirsch	DIPTERA	Tabanidae Nemestrinidae Bombyliidae Calliphoridae Sarcophagidae Tachinidae	Present paper Present paper Present paper Present paper Present paper Present paper
B. ugandensis Turner	DIPTERA	unspecified	Carpenter (1920)

*Prey of *B. bequaerti dira* and *B. braunsii* other than Tabanidae are noted jointly as "Bombyliidae, Syrphidae, Stratiomyidae, Muscoidea, etc.".

rhapha, the Syrphidae and the muscoid families Muscidae, Calliphoridae, Sarcophagidae and Tachinidae are predominant.

It is clear that the complex of flies captured by a provisioning female *Bembix* is in the first instance circumscribed by the composition of the dipterous fauna of her nesting area. The composition of the prey is further determined by the species assemblages occurring at certain sources of flies (e.g. flowers, carcases, dung, warm blooded animals, aggregations on vegetation of newly emerged flies) discovered and then repeatedly revisited by an individual hunting

female. Furthermore, as indicated by Evans, the composition of the prey may reflect innate differences in hunting behaviour amongst various *Bembix* species.

Among the presently listed species, *B. olivata* Dahlbom in the Cape Province was recorded by Ullyett and De Vries (1940) to "have been seen to frequent the vicinity of sheep during periods of blowfly [*Lucilia sericata* (Meigen)] abundance and to search around the sheep itself for flies". Blood-sucking tsetse flies, *Glossina palpalis* (Robineau-Desvoidy) in Uganda were reported by Carpenter (1920) to have been hunted on himself by *B. forcipata* Handlirsch. Similarly, *B. moebii* Handlirsch in the Transvaal was observed by Dyce catching Tabanidae feeding on cattle. On the other hand, speculation upon the origin of Tabanidae of both sexes recovered from the nests of *B. bequaerti dira* Arnold at Stanleyville (now Kisangani in Zaire) and listed by Bequaert (1932: 3) led Oldroyd (1954: 35–37) to suggest that the wasps were collecting their prey from the forest canopy or from intermediate levels.

From a consideration of at least the brachycerous component of its prey assemblage *B. albofasciata* at Hilton and Slaaikraal would appear to hunt close to the ground in the general vicinity of its nesting areas. Thus the tabanid *Chrysops obliquefasciata* Macq., the mydid *Nomoneura caffra* Hesse, the asilids *Stenopogon dilutus* (Walker), *Acnephalum andrenoides* (Wied.) and *Synolcus* sp., and the bombyliids *Lomatia pictipennis* (Wied.), *Henica longirostris* (Wied.) and species of *Systoechus, Exoprosopa* and *Villa* are well known to the author as common members of the community of insects associated with the sandy areas in which occur also the nests of *B. albofasciata*. It is only in these sandy areas that these flies of differing behaviours may be found together: all are to be found resting upon the ground or flying about low over it. All but the mydid occur in the open; the latter favours light mottled shade under clumps of *Acacia karoo* fringing the bare sandy areas.

Evans (1966: 357) has stated that "whether or not the accumulation of long lists of prey records is worth while is a moot question". Besides establishing whether the prey is dipterous, as is most often the case, it would certainly appear that such lists have little intrinsic value if what is sought from them is evidence of prey selection linked to prey systematics. On the other hand such lists, particularly where they relate to specific localities in which the ecology of the prey is known, are of use in determining patterns of hunting behaviour. Furthermore, where two or more *Bembix* species nest within the same area, they would indicate whether resource partitioning with regard to prey occurs.

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Dr F.W. GESS: 1978 –

Ethological notes on *Ceramius bicolor* (Thunberg), *C. clypeatus* Richards, *C. nigripennis* Saussure and *C. socius* Turner (Hymenoptera: Masaridae) in the Western Cape Province of South Africa

by

F. W. GESS and S. K. GESS

(Albany Museum, Grahamstown)

CONTENTS

ABSTRACT

Some aspects of the ethology of *Ceramius bicolor* (Thunberg), *C. clypeatus* Richards, *C. nigripennis* Saussure and *C. socius* Turner in the Western Cape Province of South Africa are described. Richards' (1962: 83) tentative division of the genus *Ceramius* into eight species groups is emended. Important nest characters are identified and listed under species group. Male behaviour in relation to nests is discussed.

INTRODUCTION

The present paper is the fifth in a series of publications (Gess, 1965, 1968 and 1973; Gess and Gess, 1980) dealing with the systematics and ethology of southern African species of the wasp genus *Ceramius* Latreille. In the most recent of the above listed publications accounts were given of the ethology of the three species commonly occurring in the Eastern Cape Province: *C. capicola* Brauns, *C. linearis* Klug and *C. lichtensteinii* (Klug). The findings were discussed within the context of a review of earlier published data on the nesting of *Ceramius* species (eight in all) from both southern Africa and southern Europe. Of particular interest to the present authors was the establishment of the existence amongst these species of this ground-nesting genus of differences with regard to the nest plan and the nature of the cell.

Relative lengths of shafts and whether or not a mud-cell is constructed within an excavated-cell were identified as important behavioural characters and were the starting point for two lines of thought.

Firstly, it seemed that these characters had relevance with regard to an investigation into the tentative grouping of the *Ceramius* species proposed by Richards (1962: 83) upon the basis of adult morphology. Secondly, it seemed that the form of the cell might be of interest within the context of the evolution of nesting behaviour in the Masaridae as a whole. It was found that the mud-cell constructed by *C. lichtensteinii* within the excavated-cell bears a close resemblance to the aerial cell constructed by *Pseudomasaris edwardsii* (Cresson) as described and illustrated by Torchio (1970). It is possible therefore to regard the construction of a mud-cell within an excavated-cell as being behaviourally intermediate between the excavation only of a cell and the presumably more advanced construction of an aerial mud-cell as in the genera *Geyella, Masaris, Pseudomasaris* and *Celonites*.

In order both to develop these thoughts and to answer some of the questions, details of the nesting of a greater number of *Ceramius* species will have to be obtained. To this end an expedition was undertaken during September/October, 1985 to a region rich in *Ceramius* species—that part of the Western Cape Province extending from Citrusdal in the south to Springbok in the north. Despite the consequences of a long-standing drought, the shortness of the time during which the authors were in the field (eight days) and the poor weather experienced during that time, some useful information was gathered. The nesting of two species, *C. bicolor* (Thunberg) and *C. nigripennis* Saussure was studied in fair detail, some data on the nesting of *C. socius* Turner were obtained, and an indication of the habitat preference of *C. clypeatus* Richards was gained.

As it may be some time before further species are studied in the field the publication of the presently available data is considered appropriate.

ETHOLOGICAL NOTES

Ceramius bicolor (Thunberg)

Description of nesting sites

Two nesting sites of *C. bicolor* were located. One is on a slope above the Olifants River 10 km S of Klawer on the N7 road (31° 50′S, 18° 37′E) in Acocks' Veld Type 31, Succulent Karoo (Fig. 1). This site is in a sparsely vegetated area of non-friable soil composed of clay, sand and fine gravel. This is clearly a well established nesting site as it was previously located by the first author in October, 1967 (Gess, 1968: 13). The second site is at Mesklip (29° 48′S, 17° 52′E) 20 km S of Springbok on the N7 road in Acocks' Veld Type 33, Namaqualand Broken Veld (Figs 5 and 6). This site, on the edge of a bare patch, is situated on sloping ground above a shallow farm dam the water of which at the time of the investigation was reduced to little more than wet patches. The vegetation in this area is mainly low bush, "mesems" and annual composites. The soil is non-friable and is composed of clay, coarse sand and fine gravel.

Plants visited by adult wasps and composition of provision

Males and females were recorded visiting flowers of *Psilocaulon acutisepalum* (Berger) N.E. Br. (Mesembryanthemaceae) at the Olifants River site on 27.ix.1985 (F. W. and S. K. Gess) and previously on 14/15.x.1965 (F. W. and W. H. R. Gess) (Gess, 1968: 13) and of "me-

sems with whitish flowers" at Die Bos Road (30 miles E of Clanwilliam) on 19.ix.1966 (C. D. Michener) (Gess, 1968: 13).

Pollen from the provision of the nest investigated at the Olifants River site on 29.ix.1985 was examined and found to be all of one type and identical with pollen of *Psilocaulon acutisepalum*. Pollen from the provision of one of the nests investigated at the Mesklip site on 4.x.1985 was found to be a mixture of two sizes of "mesem" pollen one of which matched that of *Psilocaulon acutisepalum*.

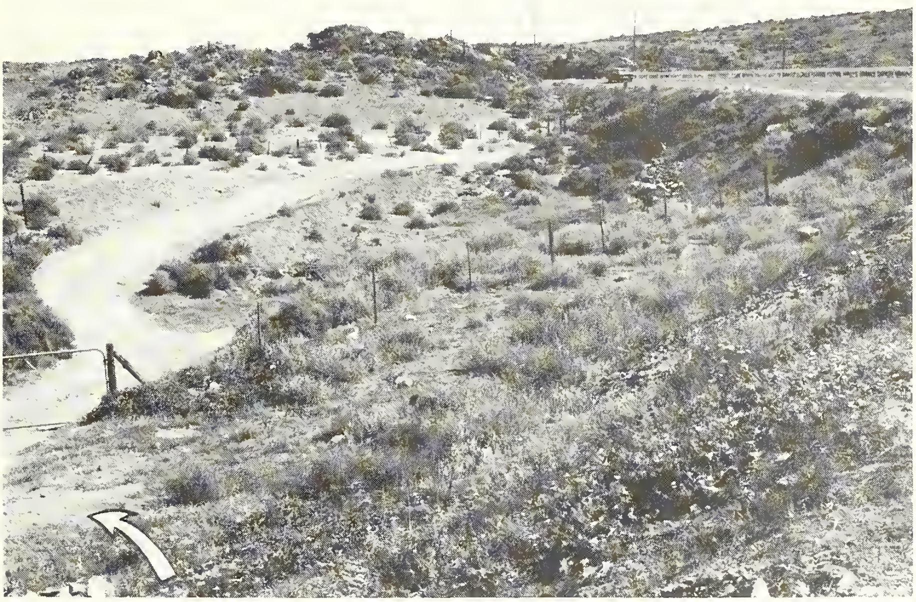


Fig. 1. Nesting area of *C. bicolor* (Thunberg) showing nesting site (arrowed) and forage plant, *Psilocaulon acutisepalum* (lower right). 10 km S of Klawer, 27.ix.1985.

Description of nest

The nest of *C. bicolor* consists of a subterranean burrow surmounted by a short curved turret constructed from mud pellets cemented together and smoothed on the inside so that in the lower part at least no interstices remain (Fig. 2). The upper part of the outer end may be extended further than the lower and be lacy in appearance.

The burrow consists of a subvertical shaft either of the same diameter as that of the turret over its entire length or over the greater part of its length but with a short bulbous enlargement near the base of the upper half. This main shaft curves to end in a subvertical to subhorizontal cell. Further cells terminating secondary shafts lie in the same plane as or below the first-excavated cell (Fig. 3).

A completed cell is sealed with a mud-plug and the section of the shaft leading to it from the vertical shaft is filled with tightly packed earth and sealed off with a thin mud plate.

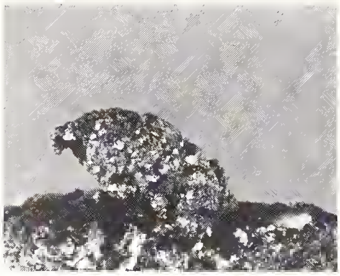


Fig. 2. Nest turret of *C. bicolor* (Thunberg) (× 2)

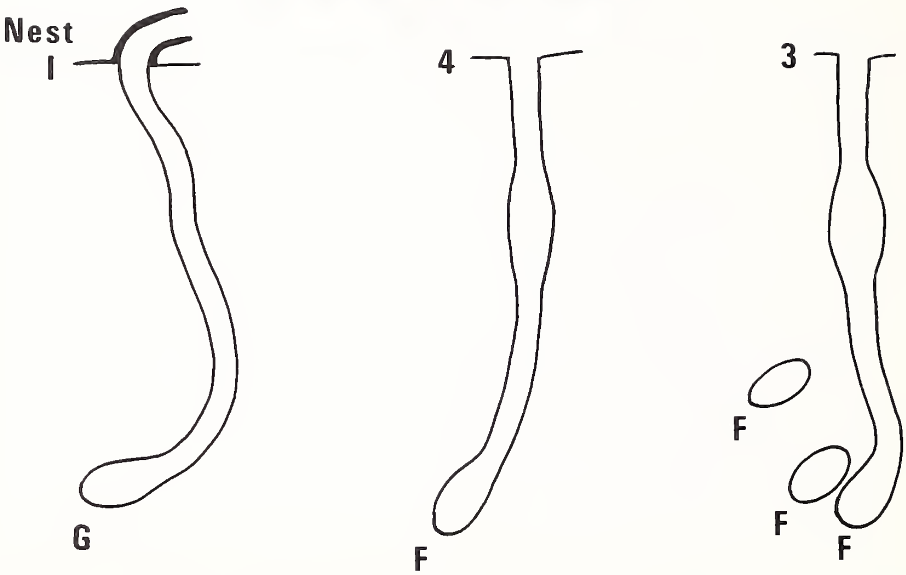


Fig. 3. Vertical plans of turrets and underground workings of nests of *C. bicolor* (Thunberg) (× 1). Nest 1, 10 km S of Klawer, 29.ix.1985; Nests 4 and 3, Mesklip, 20 km S of Springbok, 4.x.1985. For key to lettering see Table 1.

Method of construction of nest, oviposition and provisioning

Water is required for nest excavation. At an early stage in nesting a turret is constructed surmounting the shaft using pellets extracted in the course of shaft excavation. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have an inner diameter equal to the diameter of the shaft, that is 3,5–4 mm. Pellets are added more frequently to what will be the upper part of the curved turret than to what will be the lower. When turret construction is completed shaft sinking continues. Further pellets extracted are discarded. These pellets are larger than those used in turret construction.

During nest construction observed at the Olifants River site 15 pellets were extracted per water load during turret construction and only seven pellets per water load during subsequent shaft extension.

There is no set pellet dropping area. On emerging backwards from her turret carrying a

pellet the female walks to one side of the turret or up onto it and flies off in a variable direction to drop it.

In two of the four nests investigated the diameter of the shaft had been maintained at a constant 3,5–4 mm along its entire length whereas in the other two nests a bulb of 6–7 mm in diameter had been created in the upper half of the main shaft.

The first cells of the four nests ranged in depth from 58–70 mm. The average dimensions of the seven cells obtained were 6 mm by 10 mm. A mud-cell is not constructed within the excavated-cell and therefore after a cell has been excavated it is ready for oviposition. The single egg obtained was whitish, curved and 4 mm from tip to tip.

After oviposition provisioning takes place and the cell is sealed with a mud-plug. From the sealed cell the shaft leading to it is filled with tightly packed earth up to the point at which it diverges from the subvertical main shaft. The opening to the main shaft is sealed off with mud and successive secondary shafts each terminating in a cell are excavated, oviposited into, provisioned and sealed in a similar manner.

Of the four nests investigated (Table 1) two were one-celled, one was two-celled and the fourth was three-celled. In the two one-celled nests the cells were open and one contained an egg and a pollen loaf and the other a small larva and a pollen loaf. In the two-celled nest both cells were sealed and each contained a young larva and a pollen loaf. In the three-celled nest one cell was open and two were sealed. Each contained a young larva and a pollen loaf.

Table 1.

Details pertaining to the four nests of *Ceramius bicolor* investigated at 10 km S of Klawer on 29.ix.1985 (nest 1) and at Mesklip, 20 km S of Springbok on 4.x.1985 (nests 2–4).

Nest No.	Nest Status	Turret	No. of cells	Nature of each cell, cell contents	Remarks
1	New	Present	1	G	*Ceramius* ♂ in nest
2	New	Present	2	F F	—
3	New	Present	3	F F F	—
4	New	Present	1	F	*Ceramius* ♂ in nest

Key: F. Cell either open or closed, containing still feeding immature larva.
G. Cell either open or closed, containing egg with provision.

Nest-guarding behaviour

The nesting area at the Olifants River site was visited on two days, one of which (27.ix.1985) was sunny and the other (29.ix.1985) cloudy. Only on the sunny day was nest building in progress. Each nesting female was attended by a male which shadowed her whilst she was in the nesting area, even following her into the nest. When the female was away from the nesting area collecting water or foraging the male guarded the nest. The male drove off other males which came too near to the female or to the nest. Several times males were seen grappling together on the ground.

The nests at the Olifants River site and the Mesklip site were investigated on cloudy days (29.ix.1985 and 4.x.1985, respectively) when no activity outside the nests was in progress. Of the four nests investigated two contained a male each. These two nests, one at each site, both contained an unsealed but provisioned cell. No females were present in any of the nests nor were they seen in the nesting areas.

Ceramius clypeatus Richards

As no forage plants have been recorded for *C. clypeatus* it seems of interest to record the capture of two foraging males (26.ix.1985 and 28.ix.1985). Both were visiting the yellow "pea" flowers of the shrub *Aspalathus desertorum* Bol. (Leguminosae) at Klein Alexandershoek, Clanwilliam District (32° 20′20″S, 18° 46′E) lying in Acocks' Veld Type 69, Macchia (Fynbos) in the mountains between the Olifants River Valley and the coastal plain (Fig. 4). This discovery is of note due to the unusual nature of both the forage plant and the habitat. All other forage plants recorded for *Ceramius* species in South Africa are species belonging to the families Mesembryanthemaceae and Compositae. Habitats favoured by *Ceramius* species in South Africa are more usually open arid areas sparsely vegetated with low-growing species.

Fig. 4. Habitat of *C. clypeatus* Richards. Klein Alexandershoek, Clanwilliam District, 26.ix.1985.

Ceramius nigripennis Saussure

Description of nesting site

A nesting site of *C. nigripennis* was located at Mesklip (29° 48′S, 17° 52′E) 20 km S of Springbok on the N7 road in Acocks' Veld Type 33, Namaqualand Broken Veld (Fig. 5). This site is situated on sloping ground above a shallow farm dam the water of which at the time of

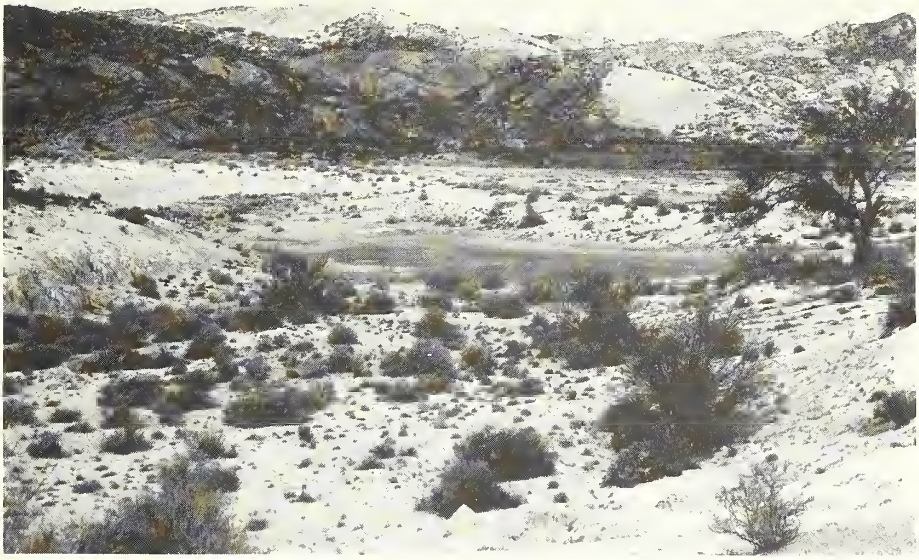


Fig. 5. Nesting area of *C. bicolor* (Thunberg) and *C. nigripennis* Saussure showing presumed water source, a shallow farm dam, in middle distance. Mesklip, 20 km S of Springbok, 4.x.1985.

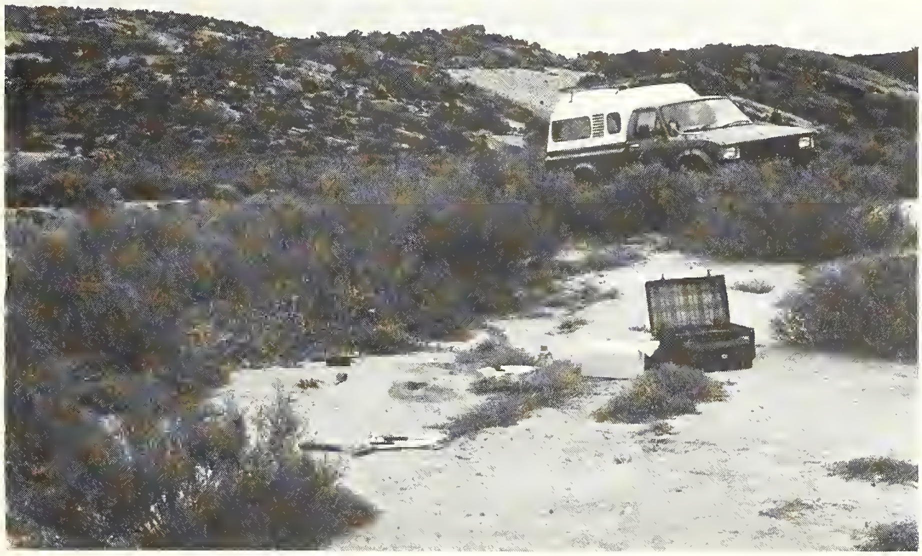


Fig. 6. Nesting site of *C. bicolor* (Thunberg) and *C. nigripennis* Saussure. Mesklip, 20 km S of Springbok, 4.x.1985.

the investigation was reduced to little more than wet patches. The vegetation is mainly low bush, "mesems" and annual composites. The soil is non-friable and is composed of clay, coarse sand and fine gravel. The sites chosen for nesting were at the edges of bare patches (Fig. 6).

Plants visited by adult wasps and composition of provision

No wasps were observed visiting plants, however, samples of pollen from the provision of two nests were compared with pollen from flowers growing in the vicinity of the nesting area. Both pollen samples were found to match the pollen of *Dimorphotheca sinuata* DC. (Compositae).

Description of nest

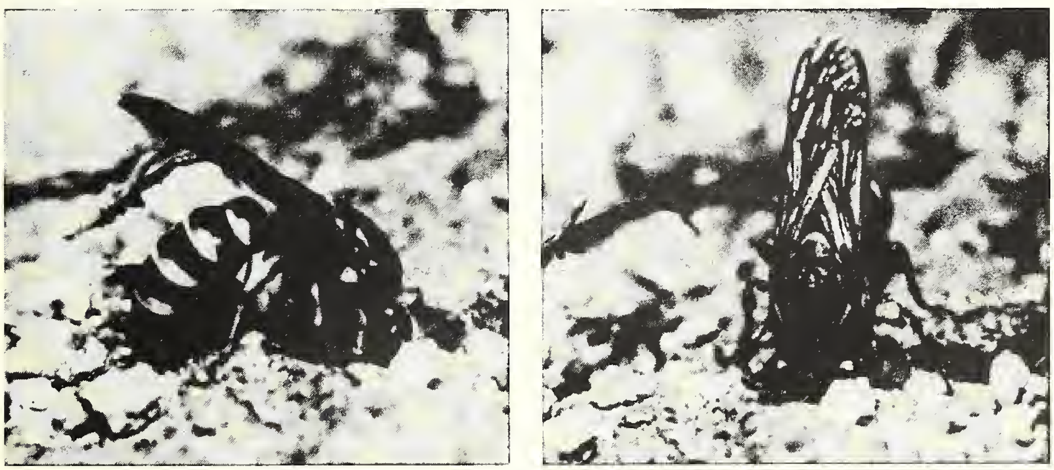
The nest of *C. nigripennis* consists of a subterranean burrow surmounted by a short cylindrical subvertical to curved mud turret constructed from mud pellets cemented together and smoothed on the inside so that few open interstices remain (Figs 7 and 19). The burrow consists of a short shaft, having the upper part of the same diameter as that of the turret and the lower of a diameter up to three times as great depending upon the number of cells present. From the base of the vase-shaped main shaft extend one or more very short subvertical secondary shafts each terminating in an excavated-cell within which is a constructed mud-cell. All the cells lie close together and all are positioned subvertically (Figs 10–13, 15). All completed cells are sealed with a mud-plug which takes the form of a stopper fitting into the neck of a cell like a cork into a bottle. The upper surface of the mud-plug is convex and rough (Fig. 14). The section of the secondary shaft between the sealed cell and the main shaft is filled with tightly packed earth and its opening to the main shaft is sealed with a thin mud plate.

Fig. 7. Part of a pseudocolony of *C. nigripennis* Saussure showing nest turrets (× *circa* 0,4). Mesklip, 20 km S of Springbok, 1.x.1985.

Method of construction of nest, oviposition and provisioning

At the commencement of nesting a female may either initiate a new nest (Figs 8 and 9) or enlarge the nest from which she emerged.

Water is required for nest construction. At an early stage in nesting both nest initiators and nest enlargers construct a turret surmounting the excavation. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have the same inner diameter as the shaft, that is 4–4,5 mm. The initial diameter of the shaft is maintained to a depth of 12 mm (average of 15, range 6–20 mm) after which the diameter is increased to form a "bulb". The main shaft is not continued below the "bulb". From the base of the "bulb" a subvertical secondary shaft of similar diameter to the entrance shaft is excavated. After a short distance, typically a few millimetres to less commonly 10 mm, the diameter is increased to create an excavated-cell. Within the excavated-cell is constructed a mud-cell. As it is probable that mud is not fetched from outside the nest it is probably mixed within the nest and as the "bulb" is of greater diameter in nests of several cells than in one-celled nests it seems likely that earth for making mud is quarried from the walls of the "bulb". Construction of the mud-cell is initiated at the bottom of the excavated-cell. Successive layers of pellets are added evenly so that the half completed cell is cup-shaped and smoothed on the inside (**Fig. 14**).



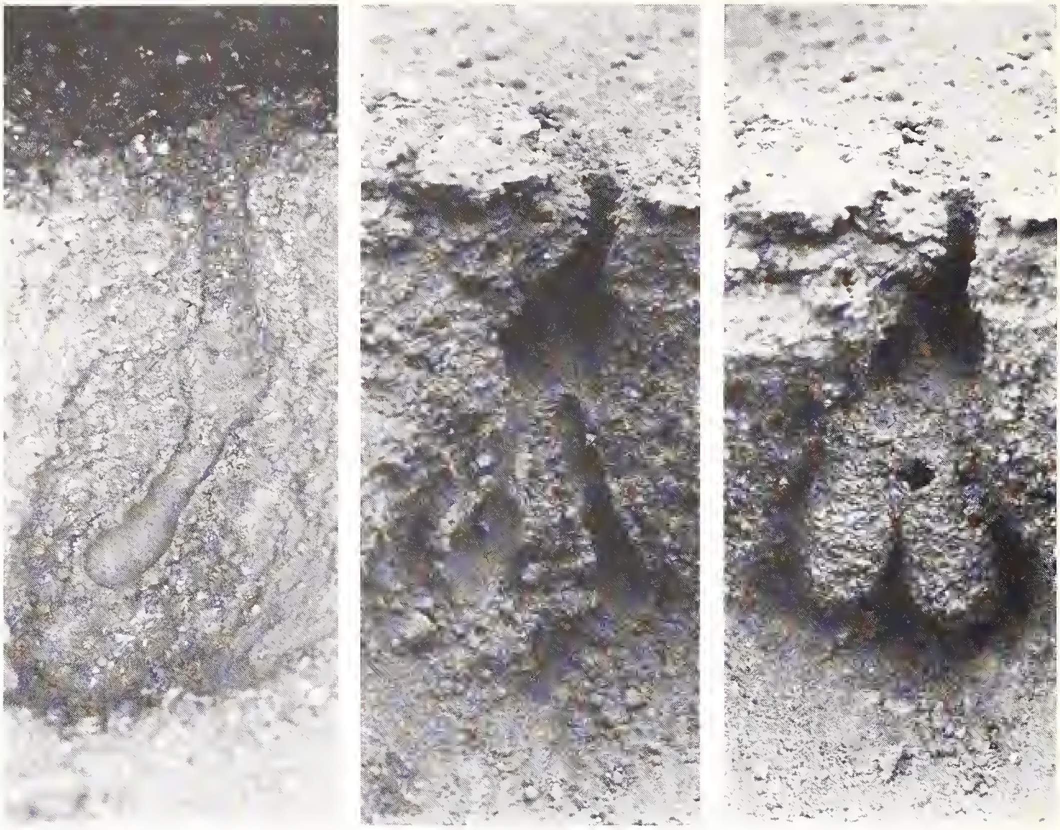
Figs 8 and 9. ***C. nigripennis*** **Saussure female initiating new nest prior to turret construction (× *circa* 3). Mesklip, 20 km S of Springbok, 1.x.1985.**

Oviposition takes place within the half-constructed cell. Five eggs were obtained. All were yellow, strongly curved, 4,5 mm from tip to tip and 1,3 mm in diameter at the mid-point.

After oviposition the construction of the cell is completed. The neck of the cell is extended into the secondary shaft so that the opening of the cell is very narrow.

Provisioning having been completed the cell is sealed with a mud-plug. The space between the mud-plug and the "bulb" is filled with earth and sealed off thinly with mud so that the entrance to the secondary shaft is no longer visible from above.

Successive cells are excavated and mud-cells constructed within them in a similar manner.



Figs 10–12. Excavations showing nests of *C. nigripennis* Saussure (× 1). Mesklip, 20 km S of Springbok, 4.x.1985. Fig. 10. Nest 3, showing a single excavated-cell containing a constructed-cell, cut through vertically. Fig. 11. Nest 1, showing two excavated-cells each containing a constructed-cell, cut through vertically. Fig. 12. Nest 1, showing two constructed-cells exposed by the removal of those shown in Fig. 11 and cleared of surrounding earth.

Seventeen nests were investigated. The number of cells per nest and the contents of the cells is indicated in Table 2. The constructed mud-cells are closely applied to the walls of the excavated-cells and their measurements therefore correspond. The outside dimensions of the constructed mud-cells were 21,7 mm by 10,5 mm (average of 30, range 16–25 mm and 10–11 mm respectively).

Nest-guarding behaviour

Only females were observed in the nesting area which was first discovered on a sunny day (1.x.1985). The wasps were all seen to be occupied in turret construction indicating that they were newly emerged. They attempted, in some instances unsuccessfully, to drive off females of *Megachile aliceae* Cockerell (Megachilidae) which were endeavouring to enter the wasp nests. Three days later (4.x.1985), on a cloudy day, 15 turreted nests were investigated. Nine of these each contained a single female. No males were found.

TABLE 2.

Details pertaining to the 17 nests of *Ceramius nigripennis* excavated at Mesklip, 20 km S of Springbok on 4.x.1985.

Nest No.	Nest Status	Turret	No. of cells	Nature of each cell, cell contents	Remarks
1	Old, reused	Present	6	A B/C B/C B/C F I	*Ceramius* ♀ in nest
2	New	Present	1	I	*Ceramius* ♀ in nest
3	New	Present	1	F	—
4	Old	Absent	6	A A A B/C B/C Y	—
5	Old, reused	Present	5	A A B/C B/C Y	*Megachile* seal in shaft
6	Old	Absent	3	C Y Y	—
7	Old, reused	Present	6	A B/C B/C B/C B/C H	*Ceramius* ♀ in nest
8	New	Present	1	H	*Ceramius* ♀ in nest
9	Old, reused	Present	3	B/C B/C Y	*Megachile* seal in shaft
10	New	Present	2	E F	—
11	New	Present	1	H	*Ceramius* ♀ in nest
12	New	Present	1	F	*Ceramius* ♀ in nest
13	New	Present	1	Z	*Magachile* ♀ in nest
14	New	Present	3	?D ?E H	*Ceramius* ♀ in nest
15	New	Present	1	?E	*Ceramius* ♀ in nest
16	New	Present	1	F	—
17	Old, reused	Present	6	A A B/C B/C E H	*Ceramius* ♀ in nest

Key: A. Cell open, containing old cocoon from which adult wasp has emerged.
B. Cell closed, containing pupa in cocoon.
C. Cell closed, containing prepupa in cocoon.
D. Cell closed, containing mature larva spinning cocoon.
E. Cell closed, containing mature larva prior to cocoon spinning.
F. Cell either open or closed, containing still feeding immature larva.
H. Cell open, containing egg without provision.
I. Cell open, empty.
Y. Old cell containing bee cell.
Z. New cell containing bee cell.

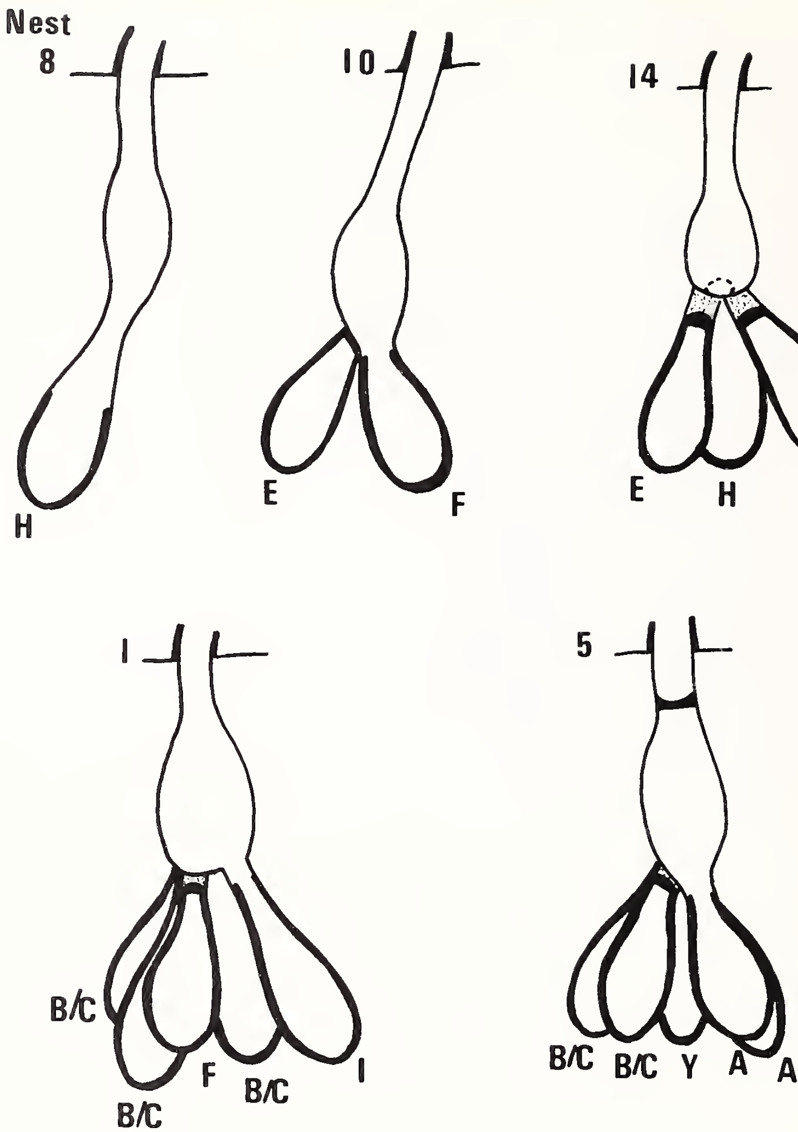
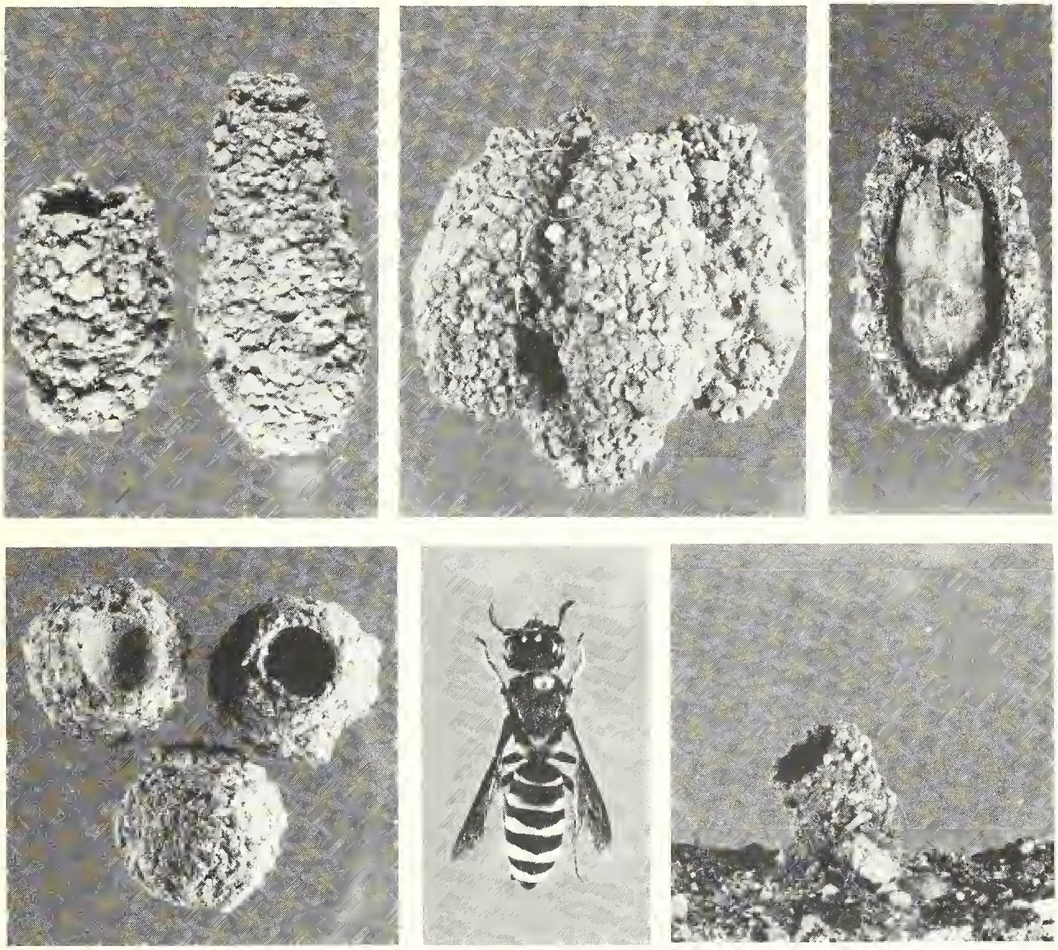


Fig. 13. Vertical plans of turrets and underground workings of nests of *C. nigripennis* Saussure (× 1). Mesklip, 20 km S of Springbok, 4.x.1985. For key to lettering see Table 2.



Figs 14–19. *C. nigripennis* Saussure constructed mud-cells, ♀ wasp, and nest turret (× 2). Mesklip, 20 km S of Springbok, 4.x.1985. Fig. 14. Half constructed mud-cell at stage at which oviposition takes place (left) and completed and sealed mud-eell showing mud-plug (right). Fig. 15. Group of four constructed mud-cells. Fig. 16. Constructed mud-cell opened vertically to show "petal" cell of *Megachile aliceae* Cockerell. Fig. 17. Upper ends of three constructed mud-cells: sealed by *Megachile aliceae* Cockerell with smooth concave mud-plug (above left); unsealed (above right); sealed by *C. nigripennis* with rough convex mud-plug (below). Fig. 18. Female wasp to show size relative to that of cells. Fig. 19. Nest turret.

Utilization of nests by a megachilid bee

It was the activity of the bee, *Megachile aliceae* Cockerell, which originally drew attention to the presence of a *C. nigripennis* pseudocolony. Several of these bees were harassing the wasps which had clearly just started nesting as all were constructing turrets. Three days later 15 turreted nests (Table 1) were investigated and of these three contained *M. aliceae* cells. In two of these nests the bee had made use of the cell from which the wasp had emerged. In both instances it was clear that the wasp had been evicted as the bee had sealed the main shaft a short

way below ground level. The third nest was newly excavated and contained a single newly constructed mud-cell in which the bee had constructed her own cell. The bee had not yet sealed her cell and was found in the nest. In addition two nests (Table 1, nests 4 and 6) from which no wasp had yet emerged in the present season were investigated. Both contained *M. aliceae* cells.

The bee cells are constructed within the mud-cells of *C. nigripennis* using the "petals" of the Namaqualand Daisy, *Dimorphotheca sinuata* DC. (Compositae), lengths of which are cut, the margins being left entire. The "petal" strips are carried into the nest cut-end first. They are arranged in such a way that a round bottomed "pot" is constructed with the "petal" strips running vertically and tucked under at the bottom of the "pot" (Fig. 16).

A cell, after provisioning and oviposition have taken place, is sealed using shorter lengths of "petal" laid cross-wise across the bee-cell opening with the ends curved upwards into the mouth of the wasp-cell which is then sealed with a mud-plug, concave above and with the surface smoothed (Fig. 17). Sealed mud-cells containing bee-cells are readily distinguishable from sealed cells of *C. nigripennis* the mud-plugs of which are convex above and with the surface left rough (Fig. 17). The bee constructs a final closure in the main shaft about 5 mm below the ground surface (Fig. 13, nest 5). This closure consists of a short length of "petal" laid across the shaft followed by a layer of mud, concave above and with the surface smoothed.

A sample of the bee provision was examined and was found to be a mixture of two sizes of "mesem" pollen.

Megachile aliceae has previously been recorded in association with burrows of *Parachilus insignis* (Saussure) (Eumenidae) in clayey soil at Hilton, Eastern Cape Province (Gess and Gess, 1976: 98). The bees had made use of burrows from which the wasps had emerged. As there is no re-use of burrows by *P. insignis* itself no competition arose.

Ceramius socius Turner

Description of nesting sites

A nesting site of *C. socius* was located on the farm Kransvlei (32° 31′55″S, 18° 50′32″E) near Clanwilliam, Western Cape Province in Acocks' Veld Types 31, Succulent Karoo / 26, Karroid Broken Veld. Nests were situated on a road verge amongst the decumbent stems of *Psilocaulon acutisepalum* (Berger) N.E. Br. (Mesembryanthemaceae) (Fig. 20). The soil was non-friable, compacted sandy clay. Water was available at a short distance, there being a trickle with puddles held back by stones on the far side of the road and another at the bottom of the road embankment.

A probable second nesting site was located on the lower slopes of the Pakhuis Pass, NNE of Clanwilliam. Holes of a suitable diameter and a dead female *C. socius* were found amongst decumbent stems of *Psilocaulon acutisepalum* on the roadside close to a recently dried up puddle.

Plants visited by adult wasps

Males and females were recorded visiting the flowers of *Psilocaulon acutisepalum* in the nesting area.

Description of nest

No completed nests were found. However, it was established that the nest consists of a subterranean burrow surmounted by a short curved mud turret constructed from mud pellets

cemented together and smoothed on the inside so that no interstices remain. The subterranean burrow of a newly constructed nest consisted of a shaft of constant diameter, vertical at first and then continuing downwards at an angle of about 50° from the horizontal. This shaft would undoubtedly have ended in an excavated-cell.

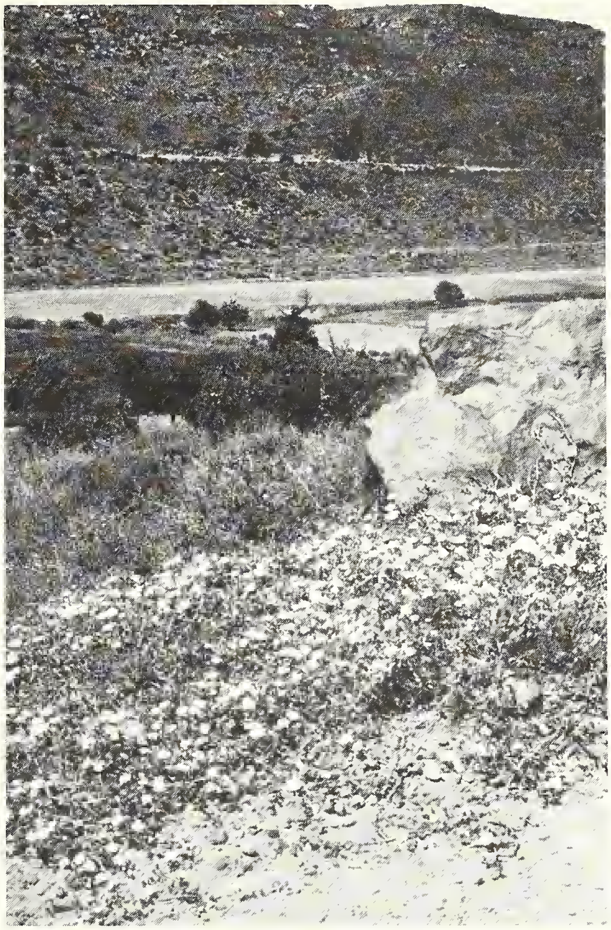


Fig. 20. Nesting area of *C. socius* Turner showing forage plant, *Psilocaulon acutisepalum* (foreground) growing over nesting site. Kransvlei near Clanwilliam, 28.ix.1985.

Method of construction of nest

Water is required for nest excavation. At an early stage in nesting a turret is constructed surmounting the shaft initial using pellets extracted in the course of shaft excavation. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will be of the same inner diameter as that of the shaft, that is 4 mm. Pellets are added more frequently to what will be the upper part of the curved turret than to what will

be the lower part. The distal opening is slightly greater, 5 mm, in diameter than the base of the turret. The rim is uneven.

After completion of turret construction pellets extracted from the shaft are discarded by the builder over a distance from just outside the turret entrance to 300 mm from the turret entrance.

Nesting was arrested by inclement weather so no nests had reached the stage of cell excavation by the close of the present investigation. The deepest burrow consisted of a main shaft of constant diameter descending vertically for 28 mm and then continuing at an angle of about 50° from the horizontal for a further 26 mm.

Activity in nesting area

At midday on a sunny day (28.ix.1985) both males and females were observed visiting flowers of *Psilocaulon acutisepalum* growing over the nesting area. Females were excavating nests and constructing turrets. No interactions were observed between males and females. On a cloudy day (29.ix.1985) the site was revisited. Females were observed sheltering head-up in nests. One nest was investigated and found to contain a single female and no male.

DISCUSSION

Before discussing the newly presented nesting data it seems useful to list the species of *Ceramius* in groups based on morphological characters. Richards (1962: 83) tentatively divided the genus into eight such groups. Of these, two (1 and 7) are constituted of Palaearctic species and the rest of Afrotropical (in effect southern African) species. The latter are here amended (taking into account Gess, 1965, 1968 and 1973) by the addition of *richardsi, rex* and *micheneri* and by the elimination of *schulthessi* (synonym of *cerceriformis*).

1. *fonscolombei* Latreille, *caucasicus* Ed. André, *bureschi* Atanassov.
2. *cerceriformis* Saussure, *clypeatus* Richards, *peringueyi* Brauns, *richardsi* Gess.
3. *nigripennis* Saussure, *toriger* Schulthess, *braunsi* Turner, *jacoti* Richards and possibly *micheneri* Gess.
4. *beyeri* Brauns and probably *damarinus* Turner.
5. *lichtensteinii* (Klug).
6. *caffer* Saussure, *metanotalis* Richards, *rex* Saussure.
7. *hispanicus* Mercet, *moroccanus* (G. Soika), *spiricornis* Saussure, *beaumonti* (G. Soika), *lusitanicus* Klug, *tuberculifer* Saussure.
8. *bicolor* (Thunberg), *linearis* Klug, *capicola* Brauns, *socius* Turner.

Nest data obtained for *C. nigripennis* (Group 3), *C. lichtensteinii* (Group 5), and *C. bicolor, C. linearis, C. capicola* and *C. socius* (all Group 8) seem to indicate that nest characters are sufficiently different between groups and similar within a group to make them useful taxonomic characters for use in conjunction with morphological characters in defining these groups. Until more information is available on the nesting of further species of *Ceramius* no characteristics possibly unique to species groups can be identified. However, it seems useful to list under group the available data on nest structure. In the presentation below the species for which data are available and the authority/authorities for the data are given for each group.

GROUP 1. *C. fonscolombei* Latreille (Fonscolombe, 1835)

a. Nest excavated in non-friable soil.

b. Burrow surmounted by a mud turret.

c–h. ?

GROUP 2. *C. cerceriformis* Saussure (Brauns, 1910)
a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c–h. ?

GROUP 3. *C. nigripennis* Saussure (Present paper)
a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. Nest perennial.
d. Nest with relatively short main shaft.
e. No cell terminating main shaft.
f. Cells terminating extremely short secondary shafts.
g. Secondary shafts subvertical and all of comparable depth.
h. A constructed mud-cell within an excavated-cell.

GROUP 4. *C. beyeri* Brauns (Brauns, 1910)
a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c–h. ?

GROUP 5. *C. lichtensteinii* (Klug) (Gess and Gess, 1980)
a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. Nest perennial.
d. Nest with relatively long main shaft.
e. No cell terminating the main shaft.
f. Cells terminating extremely short secondary shafts.
g. Secondary shafts horizontal and each successive cell deeper. The cells of any one year grouped together.
h. A constructed mud-cell within an excavated-cell.

GROUP 6.
a–h. ?

GROUP 7. *C. tuberculifer* Saussure (Giraud, 1871; Ferton, 1901)
a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c–g. ?
h. A constructed mud-cell within an excavated-cell.

GROUP 8. *C. bicolor* (Thunberg) and *C. socius* Turner (Present paper), and *C. capicola* Brauns and *C. linearis* Klug (Gess and Gess, 1980).
a. Nest excavated in non-friable soil.
b. Burrow surmounted by a mud turret.
c. Nest annual.
d. Nest with relatively long main shaft.
e. First cell terminating the main shaft.
f. Succeeding cells terminating relatively long secondary shafts.

g. Secondary shafts sloping.
h. NO constructed mud-cell within an excavated-cell.

Although a consistent picture is emerging for Group 8 in regard to nest structure there appears to be considerable variation in male behaviour within the group. The male of *C. bicolor* guards each nest under construction, frequently entering the nest with the female and remaining near or in the nest when the female is absent. On cloudy days when nesting activities cease males not females are found in nests with open cells, that is one male per nest. The males of the other three species have rarely been seen near the nests and have never been found sheltering in the nests. In these species it is the females which are found in the nests on cloudy days.

Males of *C. lichtensteinii*, Group 5, though not observed in association with nests during the study of this species (Gess and Gess, 1980) have recently been observed (at Clifton, 18 km NW of Grahamstown, Eastern Cape Province) to be constantly in attendance at nests and also to shelter in nests. However, in this species both male and female shelter in the nest.

No male behaviour was observed for *C. nigripennis* of Group 3, in fact not a single male was seen during the present study.

Attention has been drawn to the close resemblance between the constructed mud-cells of *C. lichtensteinii* and the aerial mud-cells of *Pseudomasaris edwardsii*. It has been suggested that a constructed mud-cell within an excavated-cell is behaviourally intermediate between the excavation only of a cell and the construction of an aerial mud-cell. Further, attention was drawn to the correlation between the type of cell and the length of secondary shafts (Gess and Gess, 1980), nests with no constructed mud-cell within an excavated-cell having long secondary shafts and those with a constructed mud-cell within an excavated-cell having extremely short secondary shafts. The nests of *C. lichtensteinii*, despite having extremely short secondary shafts, have relatively long main shafts so that the cells lie relatively deeply in the soil. It is of interest therefore that the nests of *C. nigripennis* have a remarkably short main shaft and that the cells are consequently close to the surface of the soil.

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A history of the collection of freshwater fishes and a catalogue of the types of freshwater fishes in the Albany Museum, Grahamstown

by

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INTRODUCTION

The aims of this paper are to present briefly the history of the fish collection in the Albany Museum and to catalogue its present type holdings. The present collection is a comparatively recent development and its type holdings have not yet been published. A number of earlier types of both marine and freshwater fishes which were originally in the Museum are no longer housed there and it is therefore necessary to clarify which types are present. The present type holdings post-date the South African Museums Association (1958, 1962) list of zoological and botanical types preserved in collections in southern and east Africa.

ABBREVIATIONS AND TERMINOLOGY

A number of different acronyms have been applied to fish specimens registered in the Albany Museum in publications since the early 1960's. In the list of zoological and botanical types published by the South African Museums Association (1962) the abbreviation AM was used to denote the Albany Museum. Fish registrations recorded by R. A. Jubb in various publications (e.g. Jubb 1964a and b, 1965a and b, 1966) were prefixed by the initials PF. This prefix was derived from the catalogue numbers of the Provincial Fisheries Institute, Lydenburg, Transvaal which supplied much of the material dealt with in these publications. [An alternative suggestion that PF refers to *Pisces Fluviatilis* is unlikely]. Skelton (1974, 1976) used the prefix AM/P for fishes registered in the Albany Museum. This prefix designated *Albany Museum/Pisces* and was used to distinguish the fish collection from other biological collections in the Museum. In more recent publications (e.g. Skelton 1984, 1985) the prefix AMSA/P was used. The SA was added to denote *South Africa* in order to avoid confusion with other institutions with similar initials such as the Amsterdam Museum in the Netherlands. Recently

Leviton *et al.* (1985) presented AMG as the official international acronym of the Albany Museum. This is a suitable acronym denoting *Albany Museum Grahamstown* and is accepted here as the standard prefix for fishes registered in this museum.

The terminology of types used in this paper follows that of the International Code of Zoological Nomenclature (3rd Edition) (1985). Type localities in the catalogue are as given in the original descriptions of the species.

HISTORY OF THE FISH COLLECTIONS IN THE ALBANY MUSEUM

Although the Albany Museum was established in 1855 the earliest reference to fish in its annual reports was in 1879 when a "curious *Ballistes conspicullum*" (a triggerfish) from the coast was presented by Dr H. Becker. Dr S. Schönland, who became "Curator" in 1889, declared in his first annual report, "I shall endeavour to form a good collection of fishes which could be of great scientific and practical importance". In 1892 he reported that the fish collection was "still small but growing steadily".

During the following decade the Museum acquired fishes mainly for display purposes. A few relics from this time have survived, for example a jar showing the embryology and development of a trout and a skeleton of the European pike, *Esox lucius,* with the skin on one side.

In October 1906 an article appeared in the Grahamstown newspaper, *The Journal,* headed "Fresh Water fishes of South Africa". The article, written by Dr J. D. F. Gilchrist of the South African Museum in Cape Town, was a call for the collection and study of freshwater fishes. The intention seems to have been for various museums in the Cape Colony, including the Albany Museum, to become regional repositories for local freshwater fishes. Response in the eastern Cape seems to have been poor.

In 1910 Mr (later Dr) J. Hewitt became Director of the Albany Museum and in his first annual report summarized the state of the various collections. The essentially marine fish collection was of minor significance. Appeals by Hewitt for freshwater fishes in 1912/13 appear to have met with little response and fishes received scant attention by the Museum until 1929 when it was first mentioned that Dr (later Professor) J. L. B. Smith of the Rhodes University College Chemistry Department was taking an interest in the fish collection. By 1930 the annual report noted that Smith had gathered and arranged all the fishes in one room of the museum. Smith was primarily interested in marine fish. In 1931 a collection of freshwater fish from the Hunyani River, Southern Rhodesia (now Zimbabwe) was contributed by Mr (later Dr) R. A. Jubb. This was the first mention of Jubb who was destined to play a major role in the history of the freshwater fish collection.

Soon after beginning to curate the fish collection Smith started to publish scientific papers on fishes. The first of these (Smith 1931) appeared in the *Records of the Albany Museum* and over the next ten years a further twenty-five papers based largely on specimens in the Albany Museum collection were published. By 1940, as a result of Smith's interest, fishes had become a leading collection in the Albany Museum. The discovery in 1939 of an extant coelacanth further inspired Smith's ichthyological interests and undoubtedly influenced his decision in 1946 to pursue this science on a full-time basis.

A fire on Saturday 6th September, 1941, destroyed many of the exhibited fishes but the study collection of fishes was preserved.

In 1946 Smith was appointed Research Professor in Ichthyology at Rhodes University College, the necessary funds being provided by the newly established Council for Scientific and

Industrial Research. In 1952 the Museum's study collection of fishes and some fish literature was entrusted on loan to Professor Smith and housed in the Ichthyology Department at Rhodes University.

In 1957 Mr and Mrs Jubb returned to Grahamstown and joined the Ichthyology Department at Rhodes University. Though by profession a meteorologist, Rex Jubb had established a reputation as an authority on the freshwater fishes of the Rhodesias and Nyasaland through numerous published articles. He and his wife made several collecting trips to various parts of southern Africa resulting in a rapid expansion of the collection. In 1961 because of a lack of storage space the Jubbs, with the freshwater fish collection, moved from their accommodation at the University to the Albany Museum. Consequently, in 1962, the Museum established a permanent post for an ichthyologist to curate, develop and research the freshwater fish collection. Mr F. L. Farquharson was appointed to this post and held it from February 1963 to the end of 1970. Jubb continued his active systematic research, publishing several papers including two important general works, Freshwater fishes of the Cape Province (Jubb 1965a) and his *magnum opus, The freshwater fishes of southern Africa* (Jubb 1967a, illustrated by H. M. Jubb). The Jubbs played an active curatorial role until the mid 1970's. Mrs Jubb's distinctive label calligraphy sets their collections apart from subsequent accessions.

Farquharson was succeeded by Mr (later Dr) P. H. Skelton who held the post from January 1972 until the end of 1983. During this period the collection grew from about 1 700 accessions to more than 10 000 making it indispensable for further systematic research on southern African freshwater fishes.

Mr J. A. Cambray took over from Skelton in 1984 and under his guidance the collection is continuing its growth.

CATALOGUE OF TYPE SPECIMENS OF FRESHWATER FISHES

ORDER CYPRINIFORMES

FAMILY CYPRINIDAE

***Barbus barnardi* Jubb 1965**

Holotype: AMG/P 1055, SL 49 mm, female.

16 Paratypes: AMSA/P 1056–1071

Collector: G. Bell-Cross, 1963.

Type locality: Mwekera Fish Farm about eight miles above confluence of Mwekera and Kafue rivers.

Reference: Jubb (1965b).

Remarks: Three paratypes are missing (Oct 1983), three paratypes decapitated, but other types are in reasonable condition.

***Barbus bellcrossi* Jubb 1964**

Holotype: AMG/P 1051, SL 40 mm, male.

3 Paratypes: AMG/P 1052–1054.

Collector: G. Bell-Cross, 14 April 1962.

Type locality: Nyakaseya, Upper Zambezi River.

Reference: Jubb (1964b).

Remarks: Holotype and two paratypes in good condition, one paratype decapitated. Six topotypes (AMG/P 1714) also present.

***Barbus bernardcarpi* Jubb 1958**
Synonym of: Barbus poechii Steindachner 1911: Greenwood (1962b).
3 Paratypes: AMG/P 309, SL 72–82 mm (Shangombo);
3 Paratypes: AMG/P 310, SL 72–89 mm (Kabuta);
3 Paratypes: AMG/P 311, SL 62–76 mm (Nampini).
Collector: Bernard Carp Expedition. July 1949, August 1952.
Type locality: Kabuta, Chobe River, Upper Zambezi River system; Nampini, Zambezi River; Shangombo, Mashi (Cuando) River.
Reference: Jubb (1958); Greenwood (1962b).
Remarks: The holotype of this species is in the J. L. B. Smith Institute of Ichthyology, Grahamstown. The paratypes are all in good condition.

***Barbus brevipinnis* Jubb 1966**
Holotype: AMG/P 1715, SL 46 mm, female.
20 Paratypes: AGM/P 1716–1735.
Collector: Provincial Fisheries Institute, Lydenburg.
Type locality: Sabi River, Incomati River system, Pilgrims Rest District.
Reference: Jubb (1966).
Remarks: Holotype and paratypes in good condition. Jubb (1966) gave incorrect registered numbers of holotype and paratypes (1072–1092).

***Barbus erubescens* Skelton 1974**
Holotype: AMG/P 2424, 84 mm SL, male.
21 Paratypes: AMG/P 2425;
2 Paratypes: AMG/P 2426;
2 Paratypes: AMG/P 2427;
2 Paratypes: AMG/P 2428;
12 Paratypes: AMG/P 2429.
Collectors: P. H. Skelton, A. Coetzer, 8 December 1973.
Type locality: Suurvlei River, Olifants River system, western Cape Province, South Africa 32° 38′ 56″S, 19° 12′ 21″E.
Reference: Skelton (1974).
Remarks: Holotype and paratypes in good condition. Other paratypes lodged in the British Museum (Natural History), London; Koninklijk Museum voor Midden Afrika, Tervuren and J. L. B. Smith Institute of Ichthyology, Grahamstown.

***Barbus tangandensis* Jubb 1954**
37 Paralectotypes: AMG/P 438.
Collector: R. A. Jubb, April 1952.
Type locality: Tanganda River about 5 miles east of its confluence with the Sabi at a spot where the water ran swiftly over a rocky bottom.
References: Jubb (1954); Greenwood (1962a).
Remarks: Jubb (1954) mentioned the original number of specimens examined to be "some 150". The AMG specimens are labelled as "Paratypes" but are, in fact, Paralectotypes as Greenwood (1962a) designated a lectotype (BMNH 1951.8.27 : 29). The British Museum collection includes four other paratypes (BMNH 1951.8.27:25–28) one of which is not a *B. tangandensis* specimen (it is probably a *B. viviparus,* pers. obs.). The Albany Museum

series is derived from two collections. One refers to an early Catalogue card F438 recorded in Jubb's handwriting which consisted of one specimen of 41 mm plus 10 more down to 23 mm. The second refers to an early Catalogue number (F538); the card, however, is missing.

***Barbus (Pseudobarbus) burchelli* A. Smith 1841**

Neotype: AMG/P 7223A, SL 102 mm, male: Skelton (1980, in prep.)

Collector: S. Thorne, 13 December 1978.

Type locality: Tradouw River, 33° 56′ 50″S, 20° 42′ 39″E, Breede River system, south-west Cape Province, South Africa.

References: A. Smith (1841); Skelton (1980, in prep.).

Remarks: It is not known which specimens A. Smith used for the original description of *Barbus (Pseudobarbus) burchelli.* This neotype was selected and designated by Skelton (1980) in a detailed taxonomic revision of the species which is in preparation for publication.

***Labeo lunatus* Jubb 1963**

Holotype: AMG/P 652, SL 244 mm, (sex not determined).

7 Paratypes: AMG/P 653.

Collector: R. A. Jubb, August 1959.

Type locality: 23 miles above Victoria Falls, Zambezi River.

Reference: Jubb (1963).

Remarks: Jubb (1963) mentions that a "metatype" was presented to the British Museum (Natural History), London. The holotype and paratypes are in good condition. The registered number was given incorrectly by Reid (1985) as SAM (P.F.) 652.

***Labeo molybdinus* Du Plessis 1963**

Holotype: AMG/P 1708, SL 218 mm, male.

Collector: S.S. du Plessis, November 1958.

Type locality: Donkerpoort Dam on the Klein Nylrivier, near Nylstroom, Transvaal.

Reference: Du Plessis (1963).

Remarks: Holotype in good condition. Two paratypes in the collection of the Transvaal Museum, Pretoria. The registered number of the holotype was given incorrectly by Reid (1985) as SAM (P.F.) 1708.

***Varicorhinus pungweensis* Jubb 1959**

4 Paratypes: AMG/P 851–854.

Collector: R. A. Jubb, May 1958.

Type locality: 18° 24′S, 32° 58′E, Pungwe River, Inyange district, Southern Rhodesia.

Reference: Jubb (1959).

Remarks: Holotype in J. L. B. Smith Institute of Ichthyology, Grahamstown. Paratypes in moderate-poor condition, largest dissected from left side in branchial region with left operculum missing. Three small specimens of unknown provenance are included with the paratypes.

ORDER SILURIFORMES

FAMILY BAGRIDAE

***Gephyroglanis barnardi* Skelton 1981**
Synonym: Austroglanis barnardi: Skelton *et al.* (1984).
Holotype: AMG/P 7647(a), SL 68.5 mm, male.
7 Paratypes: AMG/P 893 (2 cleared and stained);
14 Paratypes: AMG/P 1369;
3 Paratypes: AMG/P 1879 (4 cleared and stained).
Collector: K. C. D. Hamman and S. C. Thorne, 3 September, 1979; F. L. Farquharson, 7 April 1967; K. van Rensburg, 17 March 1965.
Type locality: Noordhoeks River at roadbridge, 32° 42′ 15″S, 19° 03′ 59″E, tributary of Olifants River, Cape Province, S.A.
Reference: Skelton (1981); Skelton *et al.* (1984)
Remarks: Holotype and paratypes in good condition, some paratypes are dissected. Paratypes also lodged in British Museum (Natural History), London; United States National Museum, Washington; National Museum of Natural History, Paris; J. L. B. Smith Institute of Ichthyology, Grahamstown; and the South African Museum Collection (in Albany Museum, Grahamstown).

FAMILY AMPHILIIDAE

***Amphilius laticaudatus* Skelton 1984**
Holotype: AMG/P 5815(A), SL 51.5 mm, female.
2 Paratypes: AMG/P 5816.
Collector: G. Bell-Cross, 6 August 1972; 15 August 1972.
Type locality: Buzi River at bridge on Inchopo to Lourenço Marques road, Mozambique, 19° 55′S, 34° 15′E, also 19 km above new Revue River bridge, Revue River, Buzi River system, Mozambique, 19° 10′S, 33° 15′E.
Reference: Skelton (1984).
Remarks: Holotype and paratypes in good condition.

***Amphilius cryptobullatus* Skelton 1985**
7 Paratypes: AMG/P 8443 (2 cleared and stained).
Collector: E. K. Balon and D. Stewart; 18 November 1970.
Type locality: Luongo River, Upper Zaire system, above and at Route 74 crossing, 10° 11′S, 29° 43′E, Zambia.
Reference: Skelton (1985).
Remarks: The holotype and further paratypes are in the Royal Ontario Museum, Toronto; paratypes are lodged in the British Museum (Natural History), London; the United States National Museum, Smithsonian Institution, Washington DC; and the J. L. B. Smith Institute of Ichthyology, Grahamstown.

FAMILY CLARIIDAE

***Clariallabes platyprosopos* Jubb 1964**
Holotype: AMG/P 1050, SL 258 mm, female.
Collector: T. E. Davidson, 1955.

Type locality: Upper Zambezi River about 15 miles above the Victoria Falls, Rhodesia.
Reference: Jubb (1964a).
Remarks: Described from the holotype only. The head of this specimen is almost severed from the body and the left gill arches are removed.

FAMILY MOCHOKIDAE

***Chiloglanis bifurcus* Jubb and Le Roux 1969**
Holotype: AMG/P 996, SL 68 mm, male.
6 Paratypes: AMG/P 997;
3 Paratypes: AMG/P 1365.
Collector: I. G. Gaigher, 14 September 1965.
Type locality: Crocodile River, Incomati River system, Montrose farm, Nelspruit district.
Reference: Jubb and Le Roux (1969).
Remarks: Holotype and paratypes in good condition, five paratypes dissected.

***Chiloglanis carnosus* Roberts and Stewart 1976**
1 Paratype: AMG/P 2741.
Collectors: T. R. Roberts, and D. J. Stewart, 4–6 August or the 12 July, 1973.
Type locality: Near village of Inga a few kilometres upstream and on the opposite side of the river (Zaire) from the Inga hydroelectric dam. Lat. 5° 27.5′S, Long. 13° 36′E; about 4–5 km upstream from Kinganga. Lat. 5° 16′S, Long. 13° 47′E; near Inga hydroelectric dam. Lat. 5° 31.5′S. Long. 13° 37.5′E; Near Tadi, about 50 km downstream from Luozi. Lat. 5° 14′S, Long. 13° 56′E.
Reference: Roberts and Stewart (1976).
Remarks: Specimen in good condition. Presented to Albany Museum on exchange by Museum of Comparative Zoology, Harvard, U.S.A. (ex. MCZ 50465).

***Chiloglanis emarginatus* Jubb and Le Roux 1969**
Holotype: AMG/P 953, SL 57.5 mm, female.
9 Paratypes: AMG/P 954.
Collector: I. G. Gaigher, 15 May 1967.
Type locality: Lekkerloop River, tributary of the Komati River of the Incomati River system, on the farm Vergelegen, Carolina district.
Reference: Jubb and Le Roux (1969).
Remarks: Holotype and paratypes in good condition. Three topotypes are also included in the Albany Museum collection (AMG/P 1747).

***Chiloglanis paratus* Crass 1960**
1 Paratype: AMG/P 886.
Collector: T. F. Elphick, 28 March 1958.
Type locality: Concrete wall of Pongola River barrage, altitude 1000 ft (31° 30′S, 27° 23′E).
Reference: Crass (1960).
Remarks: Specimen in good condition. This paratype taken from Crocodile River, eastern Transvaal. The holotype and other paratypes of *C. paratus* are in the Natal Museum collection (NMP 1408 Type No. 1154) housed at present in the Albany Museum.

ORDER CYPRINODONTIFORMES

FAMILY APLOCHEILIDAE

***Nothobranchius furzeri* Jubb 1971**
Holotype: AMG/P 1239, SL 44 mm, male.
9 Paratypes: AMG/P 1240.
Collector: W. Warne, 12 January 1969.
Type locality: Sazale Pan approximately 21° 40′S, 31° 45′E in the Gona-re-Zhou Game Reserve, Rhodesia.
Reference: Jubb (1971).
Remarks: Holotype and paratypes are in good condition.

***Nothobranchius kirki* Jubb 1969**
Holotype: AMG/P 994, SL 37.5 mm, male.
9 Paratypes: AMG/P 995.
Collector: R. G. Kirk, 21 July 1966.
Type locality: Pool adjacent to the Likangela River which forms part of the Lake Chilwa endoreic drainage basin, Malawi.
Reference: Jubb (1969).
Remarks: Holotype and 3 Paratypes are dissected. AMG/P 995 incorporates AMG/P 784.

ORDER PERCIFORMES

FAMILY CICHLIDAE

***Chetia brevis* Jubb 1968**
Synonym: Astatotilapia brevis: Greenwood (1979).
Holotype: AMG/P 951, SL 128 mm, male.
5 Paratypes; AMG/P 952.
Collector: I. G. Gaigher, September 1967.
Type locality: the Lomati River, Barberton District, a tributary of the Incomati River which enters the sea near Lourenço Marques, Mozambique.
Reference: Jubb (1968); Greenwood (1979).
Remarks: Jubb (1968) reported on 10 paratypes in AMG/P 952 and one deposited in the British Museum (Natural History), London. Four paratypes are therefore missing. Holotype and paratypes are in reasonably good condition.

***Serranochromis meridianus* Jubb 1967**
Holotype: AMG/P 913, SL 300 mm, male.
24 Paratypes: AMG/P 914.
Collector: I. G. Gaigher, April 1967.
Type locality: the Sabie River in the region of its confluence with the Sand River, both being tributaries of the Incomati River which enters the sea near Lourenço Marques, Mozambique.
Reference: Jubb (1967b).
Remarks: Holotype dissected, two paratypes decapitated, pharyngeal bone, gill arch and

lower jaws removed from one. One paratype cleared and stained. Jubb (1967) reports that one paratype is deposited in the British Museum (Natural History), London.

FAMILY GOBIIDAE

***Silhouettea sibayi* Farquharson 1970**
Holotype: AMG/P 1100, SL 27 mm, male.
4 Paratypes: AMG/P 1101, AMG/P 1102, AMG/P 1103, AMG/P 1104.
Collector: Rhodes University Ecological Survey, 18 January 1966.
Type locality: Eastern shore of Lake Sibayi (27° 21′S, 32° 47′E).
Reference: Farquharson (1970).
Remarks: Holotype and paratypes are in moderately good condition.

ORDER SYNBRANCHIFORMES

FAMILY MASTACEMBELIDAE

***Mastacembelus vanderwaali* Skelton 1976**
Synonym: Afromastacembelus vanderwaali: Travers (1984).
Holotype: AMG/P 3183(a), SL 153 mm, male.
11 Paratypes: AMG/P 3183(b);
15 Paratypes: AMG/P 3450 (5 cleared and stained);
5 Paratypes: AMG/P 2712 (1 cleared and stained);
3 Paratypes: AMG/P 3296.
Collectors: B.C.W. van der Waal, P. H. Skelton, 29 September 1975.
Type locality: Zambezi River mainstream, at Katima Mulilo, Eastern Caprivi. Approximately 17° 30′S, 24° 16′E.
Reference: Skelton (1976); Travers (1984).
Remarks: Holotype and paratypes in good condition. Other paratypes deposited in British Museum (Natural History), London (5); American Museum of Natural History, New York (5); J. L. B. Smith Institute of Ichthyology, Grahamstown (3); Queen Victoria Museum, Harare (collection now in National Museum, Bulawayo) (14). Skelton (1976) recorded 3 paratypes with reg. No. AMG/P 3396 (=3296) in error.

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Editor
Dr F.W. GESS: 1978 –

The spread of the Southern Greyheaded Sparrow in the Cape Province

by

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ABSTRACT

The first records of the Southern Greyheaded Sparrow *Passer griseus* in Transkei, Ciskei, and Cape Province south of the Orange River are reviewed. Its increase in range in recent years is discussed in relation to the distribution of other *Passer* species.

INTRODUCTION

The Southern Greyheaded Sparrow is one of a group of five very similar birds which some authorities place as subspecies of the Greyheaded Sparrow *Passer griseus* (Clancey, 1980) and others treat as full species (Hall and Moreau, 1970). The grey-headed sparrows are birds of grassland and lightly-wooded savanna. It is probable that the five populations were separated during the pluvial period that occurred in Africa about 10 000 years BP, when the Congo forest spread across to the east coast (Hamilton, 1982). With a subsequent drying of the climate and the retraction of the rain forest the separate populations spread so that they are now once more in contact. Grey-headed sparrows occur over all of the Afrotropical Region with the exception of the extreme south of the continent. Coincident with the change in climate there has been a spread of agriculture from the north that modified the habitat so that it became more suitable for seed-eating savanna birds. By the time that records became available the distribution of grey-headed sparrows appeared to have reached a state of equilibrium with no more than local consolidation as the birds exploited land modified by agriculture.

IDENTIFICATION

Like other sparrows the Southern Greyheaded Sparrow has plumage in which various shades of brown and grey predominate. It can be distinguished from the other members of the genus *Passer* found in the Cape Province—the Cape Sparrow *P. melanurus*, the House Sparrow *P. domesticus* and the Great Sparrow *P. motitensis*—by a conspicuous white wing-bar, uniform grey head with no eye-stripe, and the absence of any black markings on the throat. The sexes of the Southern Greyheaded Sparrow are similar in plumage, but in the Cape, House and Great sparrows the males have a conspicuous black patch on the throat.

SOURCES OF THE DATA

In addition to published records, the analysis is based on information obtained from specimen collections (particularly that of the East London Museum), together with the personal observations of two of the authors (A.Craig and B.Every) and local correspondents. Localities were determined using Leistner and Morris (1976), Skead (1973) and 1 : 50 000 maps.

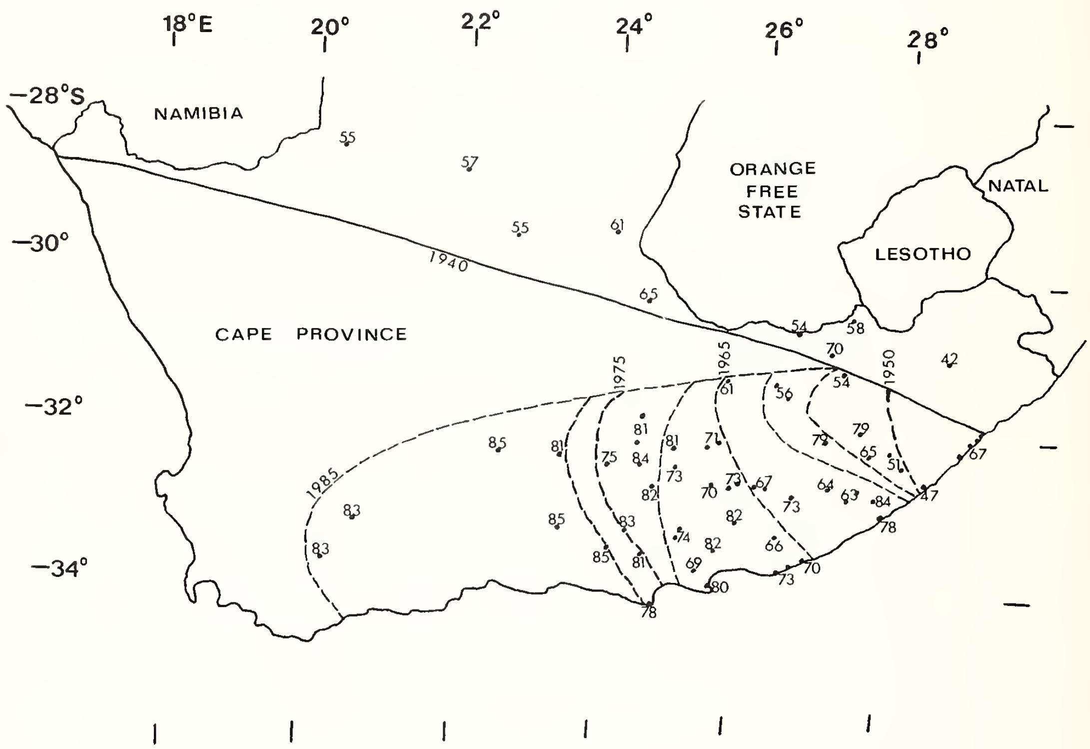

Fig. 1. The spread of the Southern Greyheaded Sparrow in the Cape Province. The last two figures of the year of the first-recorded occurrence are shown at selected point localities, and the tentative western limits at 5-year intervals from 1950 onwards are indicated by dashed lines.

TABLE 1

First-recorded occurrences of the Southern Greyheaded Sparrow in the Cape Province south of the Orange River, in the Transkei and in the Ciskei.

Locality	Date	Reference
Philipstown 30° 26′S 24° 28′E	1915	Hare, 1915
Sulenkama 31° 01′S 28° 41′E	08.10.42	Crass, 1944
Kobonqaba River mouth 32° 36′S 28° 29′E	1947	Pike, 1965
Nqamakwe, Blythswood Mission 32° 13′S 27° 59′E	1951	Pike, 1952
Umtata 31° 36′S 28° 49′E	02.02.53	C. J. Skead (pers. comm.)
Strydpoort, Rossouw 31° 10′S 27° 16′E	06.05.54	E. L. Museum
Aliwal North 30° 42′S 26° 43′E	12.10.54	E. L. Museum
Augrabies 28° 54′S 20° 19′E	14.09.55	E. L. Museum
Prieska 29° 40′S 22° 45′E	18.09.55	E. L. Museum
Buffelsfontein 31° 24′S 26° 22E	1956	S. Stretton in Every, 1982a
Karas, Upington 28° 28′S 21° 14′E	01.11.57	E. L. Museum
Groblershoop 28° 55′S 22° 00′E	03.11.57	E. L. Museum
Telle River, Sterkspruit 30° 31′S 27° 22′E	25.03.58	E. L. Museum
Teebus 31° 22′S 25° 40′E	26.08.61	E. L. Museum
Hopetown 29° 37′S 24° 05′E	29.08.61	E. L. Museum
Lyndoch Farm, Bedford 32° 30′S 26° 01′E	25.11.62	C. J. Skead (pers. comm.)
Keiskammahoek 32° 41′S 27° 09′E	26.12.62	Skead, 1964
Kei Road 32° 42′S 27° 33′E	18.08.63	Skead, 1970
Imvani 32° 02′S 27° 04′E	11.01.64	C. J. Skead (pers. comm.)

Locality	Date	Reference
Halcyon Drift 30° 57′S 28° 27′E	28.09.64	C. J. Skead (pers. comm.)
Bethulie Bridge 30° 34′S 26° 02′E	12.01.65	C. J. Skead (pers. comm.)
Bolo-Kei Bridge, Stutterheim 32° 15′S 27° 40′E	07.04.65	E. L. Museum
Adelaide 32° 42′S 26° 17′E	1965	Pike, 1965
Grahamstown 33° 18′S 26° 32′E	mid-1966	Tree, 1973
Mount Ayliff 30° 48′S 29° 23′E	14.04.67	E. L. Museum
Xora River mouth 32° 09′S 29° 00′E	15.06.67	E. L. Museum
Umtata River mouth 31° 57′S 29° 11′E	29.06.67	E. L. Museum
The Haven, Butterworth 32° 14′S 28° 55′E	1967	C. J. Vernon (pers. comm.)
Uitenhage 33° 46′S 25° 25′E	12.69	Every, 1973
Floukraal 30° 58′S 27° 05′E	07.11.70	E. L. Museum
Port Alfred 33° 36′S 26° 54′E	1970	Every, 1981a
Katkop 30° 52′S 28° 31′E	04.71	Every, 1973
Mountain Zebra National Park 32° 15′S 25° 27′E	1971	McGill, 1971
Mount Fletcher 30° 41′S 28° 30′E	04.10.72	E. L. Museum
Fort Beaufort 32° 47′S 26° 38′E	13.03.73	E. L. Museum
Lake Mentz 33° 10′S 25° 08′E	10.73	Martin and Martin, 1975
Cranemere Farm 32° 31′S 25° 00′E	14.11.73	E. Pike (pers. comm.)
Cookhouse 32° 45′S 25° 49′E	1973	Brown, 1973
Kenton-on-Sea 33° 41′S 26° 40′E	1973	Bennett, 1975
Glenconner 32° 24′S 25° 09′E	02.10.74	Martin and Martin, 1975

Locality	Date	Reference
Aberdeen 32° 29′S 24° 04′E	30.03.75	Brown, 1975
Hopeleigh, Salem 33° 27′S 26° 29′E	06.02.77	Sulter, 1977
Cambridge, East London 33° 01′S 27° 55′E	30.06.78	C. J. Vernon (pers. comm.)
Cape St Francis 34° 12′S 24° 52′E	12.78	J. Estcourt in Every, 1981a
Gonubie 32° 56′S 28° 01′E	02.02.80	C. J. Vernon (pers. comm.)
Komga 32° 35′S 27° 55′E	04.03.80	C. J. Vernon (pers. comm.)
Port Elizabeth 33° 58′S 25° 36′E	03.80	A. Odgers in Every, 1981a
Visrivier 31° 55′S 25° 25′E	21.05.80	C. J. Vernon (pers. comm.)
Fort Brown 33° 08′S 26° 38′E	04.06.80	C. J. Vernon (pers. comm.)
Badi 32° 01′S 28° 35′E	13.10.80	C. J. Vernon (pers. comm.)
Breakfast Vlei 33° 05′S 26° 57′E	02.11.80	C. J. Vernon (pers. comm.)
Nieu-Bethesda 31° 52′S 24° 34′E	31.03.81	C. J. Vernon (pers. comm.)
Spitskopvlei 31° 55′S 25° 13′E	31.03.81	C. J. Vernon (pers. comm.)
Swaershoek 32° 30′S 25° 25′E	18.08.81	C. J. Vernon (pers. comm.)
Kleinplaats 33° 39′S 24° 37′E	17.09.81	Martin *et al.*, 1981
Addo Elephant National Park 33° 30′S 25° 45′E	09.81	Grobler and Braack, 1984
Bokvlei 32° 26′S 23° 22′E	27.10.81	Every, 1981b
Petersburg 32° 18′S 24° 58′E	09.11.81	C. J. Vernon (pers. comm.)
Graaff-Reinet 32° 15′S 24° 32′E	11.11.81	C. J. Vernon (pers. comm.)
Kroomie 32° 46′S 26° 27′E	13.11.81	C. J. Vernon (pers. comm.)
Rhodes 30° 48′S 27° 58′E	19.12.81	C. J. Vernon (pers. comm.)

Locality	Date	Reference
Elands Height 30° 48′S 28° 13′E	11.01.82	C. J. Vernon (pers. comm.)
Naudesnek 30° 43′S 28° 07′E	11.01.82	C. J. Vernon (pers. comm.)
Toleni 32° 27′S 27° 51′E	13.02.82	C. J. Vernon (pers. comm.)
Addo 33° 33′S 25° 41′E	12.04.82	Every, 1982a
Mpetu 33° 39′S 28° 05′E	27.06.82	C. J. Vernon (pers. comm.)
Fraser's Camp 33° 18′S 26° 54′E	11.08.82	C. J. Vernon (pers. comm.)
Kommadagga 33° 10′S 25° 55′E	22.08.82	C. J. Vernon (pers. comm.)
Toise 32° 24′S 27° 17′E	31.08.82	C. J. Vernon (pers. comm.)
Golden Valley 32° 56′S 25° 58′E	15.10.82	C. J. Vernon (pers. comm.)
Queenstown 31° 54′S 26° 53′E	15.11.82	C. J. Vernon (pers. comm.)
Harefield 32° 45′S 24° 40′E	1982	T. Hobson in Every, 1982b
Matjiesfontein 33° 14′S 20° 35′E	05.03.83	C. J. Uys per A. Craig
Piggott's Bridge 33° 06′S 26° 26′E	10.04.83	C. J. Vernon (pers. comm.)
Cathcart 32° 18′S 27° 09′E	04.83	D. Boddam- Whetham in Every, 1985a, b
Montagu 33° 47′S 20° 07′E	20.10.83	J. Martin per A. Craig
Herbert's Hope 32° 52′S 26° 09′E	25.10.83	C. J. Vernon (pers. comm.)
Steytlerville 33° 20′S 24° 21′E	13.12.83	C. J. Vernon (pers. comm.)
Riebeeck-Oos 33° 12′S 26° 10′E	05.08.84	C. J. Vernon (pers. comm.)
Ebenezer 32° 33′S 24° 54′E	19.08.84	C. J. Vernon (pers. comm.)
Kendrew 32° 31′S 24° 30E	29.08.84	C. J. Vernon (pers. comm.)
Mjika 31° 25′S 28° 40′E	21.11.84	C. J. Vernon (pers. comm.)

Locality	Date	Reference
Macleantown 32° 25′S 28° 40′E	1984	Hill, 1985
Baviaanskloof 33° 37′S 24° 07′E	07.02.85	D. Hall in Every, 1985a
Beaufort West 32° 12′S 22° 35′E	03.85	A. Craig

FINDINGS

Records are plotted in Fig. 1. The solid line shows the probable southern limit of the Southern Greyheaded Sparrow in about 1940 (McLachlan and Liversidge, 1957). The dates of first appearances south of this line are indicated on Fig. 1 and full details of the localities identified as the first records for each quarter-degree square are listed in Table 1 to make them available for future reference. No distinction has been made between first appearances and breeding records. The Southern Greyheaded Sparrow is largely sedentary. In most cases it appears to have settled down and bred very soon after having been recorded in a new area (Every, 1976b and Jubb, 1976).

One should not expect the records to show a clear, advancing front as they are strongly influenced by chance and the distribution of observers, and furthermore some later filling in of the area behind the vanguard will obviously occur. However, by concentrating on the most westerly records the probable boundary of the spread has been sketched at 5-year intervals from 1950 onwards (Fig. 1). If the records are complete this suggests an overall average advance of about 20 km/year for the period 1950 to 1980 with an increase in rate to 75 km/year over the last five years. At this rate the birds will soon reach Cape Town in the extreme southwest.

DISCUSSION

The members of the genus *Passer* are successful and adaptable birds. Of 20 species (recognising the five grey-headed sparrows as separate species) no fewer than eight have shown significant increases in their distributional ranges since 1950 (Summers-Smith, in press). For two species, the House Sparrow and the Tree Sparrow *P. montanus*, the spread has been primarily the result of introductions to new areas, either deliberate or accidental (Long, 1981). For the most part the birds have responded to man-induced changes in the environment or modified their own habitat preferences. Forest clearance allowed the Pegu Sparrow *P. flaveolus* of Indo-China to spread south into the Malaysian peninsula (Ward, 1968), and the Cape Sparrow spread into the vineyards in the southwestern Cape following changes in viticultural practice (Siegfried, 1973).

In the first guide to the Eastern Cape avifauna, Hewitt (1931) mentioned in a footnote that the Greyheaded Sparrow might occur near the Orange River. The only specimens in the Albany Museum collection date from Hewitt's time, but they are from Malawi. Skead (1965) did not record Greyheaded Sparrows in the Albany (Grahamstown) district but did report occasional sightings in the King William's Town area in which in addition nesting was first ob-

served in 1968 (Skead, 1964 and 1970). Subsequently Skead (1967) provided a thorough review of bird distribution in the Eastern Cape Province in which he commented on some recent southerly records of the Greyheaded Sparrow " . . . . whether this is due to a slow and recent spread or whether the bird has been overlooked is not known." Markus (1967) identified specimens of this species from the Bedford district and noted that there were at that time no records from localities such as Grahamstown, Port Alfred, East London and Uitenhage. Every (1976a) collated the available records of Greyheaded Sparrows in the Eastern Cape and showed clearly that its range was increasing.

No obvious reason for the spread of the Southern Greyheaded Sparrow is apparent although it seems most likely that it is associated with subtle changes in land use. Another species which has shown a westward expansion in recent years is the Hadeda Ibis *Bostrychia hagedash,* however, in this case there appears to be a clear correlation with human settlement and agricultural practices (Macdonald *et al.*, 1986). The Greyheaded Sparrow has moreover moved into an area already occupied by potentially competitive congeners, the indigenous Cape Sparrow and the House Sparrow, which quite recently spread through the area now being colonised by the Greyheaded Sparrow (Vierke, 1970).

Irwin (1981) implies that in Zimbabwe the Greyheaded Sparrow is being replaced around human settlements by the House Sparrow. Similarly Benson and Benson (1977) noted that in Malawi the Greyheaded Sparrow was probably originally a woodland species which had taken advantage of habitat changes resulting from agriculture. They suggested that competition with House Sparrows for nest sites would result in the displacement of the Greyheaded Sparrow.

The situation in the Cape Province provides little support for the idea that interspecific competition is important in determining the distribution of the *Passer* species. At Table Farm near Grahamstown, Greyheaded and House sparrows feed and breed side by side in the farmyard and on the outbuildings. In Grahamstown itself, the House Sparrow is largely restricted to the commercial centre whereas the Greyheaded Sparrow is the common suburban species. Both here and in the adjacent coastal belt Cape Sparrows are localised and uncommon. In the Cradock district, Collett (1982) reported that House and Cape sparrows initially alternated in nesting at the farm homestead, but from about 1962 onwards both species nested in close proximity. Meanwhile the Greyheaded Sparrow became progressively more frequent in the area, and it now utilises similar nest sites.

The significance of interspecific competition in ecology is currently vigorously debated, as illustrated by the opposing views of Schoener (1982) and Connell (1983). Despite much speculation concerning its role in evolution, present knowledge suggests that interspecific competition is unimportant as an evolutionary factor for mobile animals (Walter *et al.*, 1984). Re-examination of some of the classical studies of niche separation in sympatric species has led to alternative explanations (Pulliam, 1985), and it is clear that many different factors can determine the outcome of interspecific interactions. The South African *Passer* species provide excellent material for comparative studies for those who do not consider sparrows unworthy of closer attention.

ACKNOWLEDGEMENTS

Carl Vernon, John Bennett, Eric Pike and Jack Skead supplied many records. Graham Ross and Carl Vernon assisted in establishing the correct co-ordinates for the records. Dorothy Pitman and Graham Pike generously provided B. Every with copies of Skead (1973) and Leistner and Morris (1976) respectively. We are most grateful to them all.

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A taxonomic revision of the redfin minnows (Pisces, Cyprinidae) from southern Africa

by

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CONTENTS

ABSTRACT

The redfin minnows of southern Africa form a distinctive group of cyprinid species traditionally placed within the genus *Barbus*. The species are distributed within the rivers of the Cape Fold Mountains in South Africa and the Drakensberg and Maluti Mountains in Lesotho. The taxonomic history of the species is reviewed with the conclusion that at least two closely similar species pairs require further taxonomic investigation. A broad based character analysis of all the species is presented and taxonomic conclusions made. The character analysis indicates that two natural groups or monophyletic lineages are present, one of which is sufficiently different from all other *Barbus* species to warrant separate generic status. The genus

This paper is dedicated to the memory of Dr R. A. Jubb (1905–1987).

Pseudobarbus is defined and redescriptions of all the redfin species are provided. A neotype is selected for *Pseudobarbus burchelli*. Aspects of the conservation of these fishes are discussed.

INTRODUCTION

This study concerns a group of cyprinid minnows, known as "redfins", which are found mainly in the streams and rivers draining the Fold Mountains of the Cape Province in South Africa. A hallmark of all the species is the bright red colour of the fins, which has resulted in the species being considered to comprise a natural (or monophyletic) group (Barnard, 1943 and Jubb, 1965 and 1967).

Barnard (1943) was the first author to recognise that there is a distinct group of redfin minnows in southern Cape freshwaters. Earlier authors, often working only with preserved specimens, did not always detect the red colour of the fins of certain species. Barnard (1943) and Jubb (1965 and 1967) resolved many of the taxonomical problems concerning redfin species. In spite of the progress by these authors some of the species required further taxonomic clarification. Other matters of a systematic nature concerning the redfins depended on the prior resolution of these basic taxonomical problems. The phylogenetic relationships of the species and their biogeography are particularly interesting in view of the remarkably integrated nature of the species as a group and their circumscribed distribution at the extreme south of the continent.

The present study deals with the taxonomy of the redfin minnows. It forms part of a broad systematic study (Skelton, 1980) that includes biogeography (Skelton, 1986), phylogeny (Skelton, in prep. a) and osteology (Skelton, in prep. b). Within the context of the phylogenetic philosophy, the taxonomy depends to a large extent on the interrelationships of the species (Wiley, 1981) and the two should be considered together. In the present case where both the in-group and out-group data baselines are comparatively weak there was a need for a detailed character based taxonomic analysis to precede the phylogenetic analysis. The results of the phylogenetic analysis are nevertheless anticipated and incorporated into the taxonomy.

TAXONOMIC HISTORY

Smith (1841) gave the first description of a redfin species *Barbus (Pseudobarbus) burchelli* noting only that it was to be found in "various rivers of the Cape Colony". An attractive but technically inaccurate illustration accompanied the description and showed clearly the red colour of the fins. Smith (1841) commented that local inhabitants referred to this species as the "rooye vlerk carper".

Castelnau (1861), in describing *Gnathendalia vulnerata*, also noted that local inhabitants used the common name "redfin". The name *Gnathendalia* referred to the Genadendal Mission station on the Riviersonderend (Breë River system) where the specimens were collected. The description was based on three skins, now in the British Museum (Natural History) (BMNH). Shortly thereafter Peters (1864) described *Barbus afer* from three specimens collected by Krebs in the 1820's (ffolliott and Liversidge, 1971) but this species was not recognised as a redfin until Jubb's (1965) study.

Günther (1868) synonomised *G. vulnerata* with *Barbus gobionides* Cuvier and Valenciennes, 1842. Type specimens of *B. gobionides* are not known to exist and Barnard (1943) considered this species to be a *nomen dubium* as the original description was not adequate to

define any redfin or other species known at the time. Steindachner (1870) described *Barbus multimaculatus* which Boulenger (1905) placed in synonymy with *B. vulneratus*. Boulenger (1911) used Steindachner's figure of *B. multimaculatus* to illustrate *B. vulneratus*.

Boulenger (1911) also described two species only subsequently recognised as redfins viz., *Barbus burgi* and *Barbus asper*. A number of identification errors made by Boulenger (1911) and repeated by Gilchrist and Thompson (1913–1917) were corrected by Barnard (1943). These included the following: four specimens of *B. burchelli* from Deelfontein are actually *Barbus anoplus* Weber,1897; *B. vulneratus* from the Baakens River are *B. afer*; the illustration of *B. anoplus* (not a redfin species) is of a *B. afer* specimen; the illustration of *B. afer* is of a juvenile *B. burgi*. In consequence of Boulenger's mistakes Gilchrist and Thompson (1913–1917) misidentified certain material and also confused specimens of *B. asper* with *B. anoplus* and thereby considered the latter to be a redfin species.

Smith (1936) described *Barbus senticeps*, a relatively large-scaled species, from the Kromme River to the west of the Gamtoos. Barnard (1938a and b) described a further four redfin species although one, *Oreodaimon quathlambae* (Barnard, 1938a), was not recognised as a redfin until the present study (Skelton, 1974a and 1976). The redfins described by Barnard (1938b) were *Barbus calidus*, *Barbus tenuis* and *Barbus phlegethon*. Barnard's (1943) revision included seven redfin species all from the rivers of the Cape Fold Mountain Belt: *B. calidus* and *B. phlegethon* (Olifants River system); *B. burchelli* (Berg and Eerste River systems); *B. vulneratus* (Breë and adjacent rivers);*B. asper* (Gourits and Gamtoos River systems with a variant form in the coastal rivers between the two systems); *B. tenuis* (Gourits River system); and *B. senticeps* (the Kromme, Baakens and Swartkops Rivers of the eastern Cape).

Jubb (1965) made several nomenclatural changes to the redfins. *Barbus afer* was substituted for *B. senticeps*, *B. burgi* replaced *B. burchelli* and *B. burchelli* replaced *B. vulneratus* which became a junior synonym. The reasons for these changes are given later in the species accounts. A few problems nevertheless remained because certain species were difficult to identify and in some cases identification depended more on the geographical origin of the specimens than anything else. Jubb (1967) also reported an unusual population of *B. calidus* which required taxonomic attention (Skelton, 1974b).

Skelton (1974a) noted that the species *Oreodaimon quathlambae* (Barnard, 1938a) has bright red patches over the basal fin areas and suggested that the species may be related to the redfins of the southern Cape. Further study supported this suggestion (Skelton, 1976) and *O. quathlambae* was therefore included in this taxonomic revision.

STUDY AREA

The redfin minnows are found in the rivers draining the Cape Fold Mountain ranges in the southern and south-western Cape Province of South Africa, as well as streams of the high Drakensberg and Maluti Mountains in Lesotho (Fig. 1).

The Cape Fold Mountains are rugged, prominent features of the landscape (Wellington, 1955 and King, 1963), rising to about 2 000 metres. They date from an early Permian orogeny (Halbich *et al.*, 1983). There are two series of ranges, a north-south belt in the west and a double arc of east-west ranges in the south and south-east. These mountains occur between the Great Escarpment and the coast, an important factor in connection with the drainage patterns. The rivers run along the strike of the valleys but in several places turn abruptly to penetrate the mountains through deep, spectacular gorges.

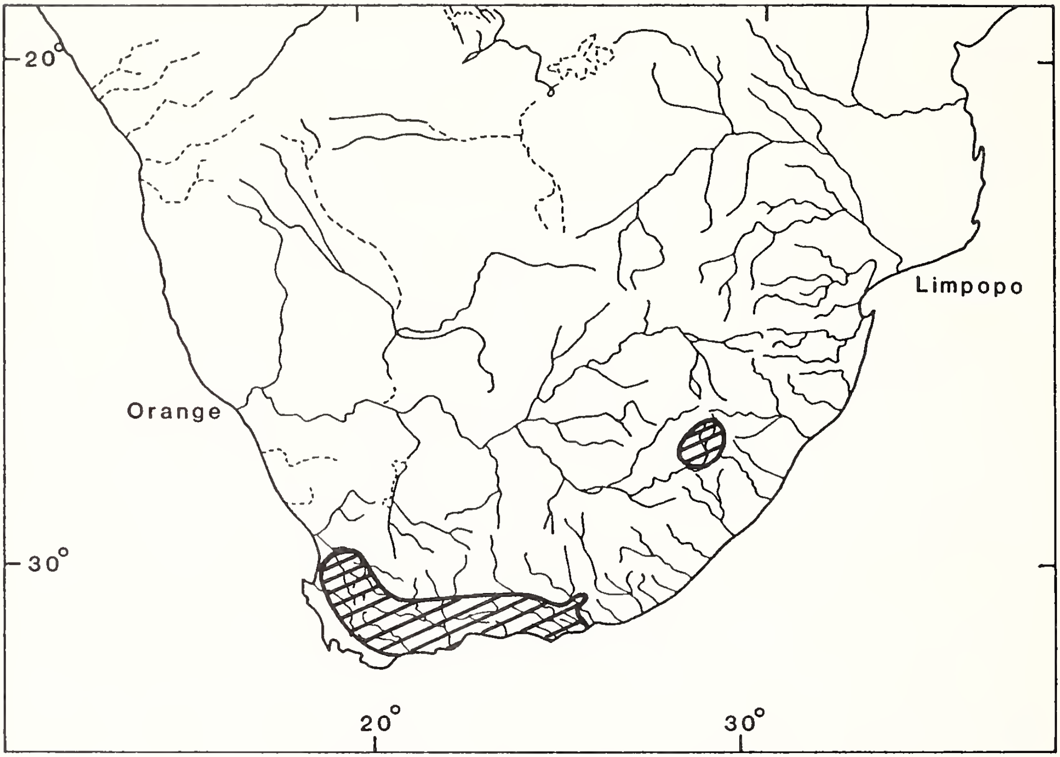

Fig. 1. The general distribution of redfin minnows in southern Africa.

The mountain ranges consist to a great extent of the resistant sandstones of the Table Mountain Group (Cape Supergroup) (Lambrechts, 1979 and Theron, 1983). These are well leached, reworked quartzitic sandstones that impart few soluble salts to the runoff water which is consequently mineral deficient, acidic and often stained brown to a greater or lesser extent (King *et al.*, 1979). The valley formations are mostly of the Bokkeveld Group consisting largely of shales of marine origin that yield waters of high salinity (Bond, 1946).

The drainage of the Fold Mountain region may be conveniently grouped into eight systems or catchment areas. There are four relatively large river systems that drain from the Great Escarpment and penetrate or pass the Fold Mountains to reach the sea. These are, from the west, the (Clanwilliam) Olifants (not to be confused with other rivers of this name in southern Africa), the Gourits, the Gamtoos and the Sundays River systems. Certain rivers adjacent to the Gamtoos and Sundays systems are included with these systems. Other major drainage areas are the west coast which includes the Berg River and adjacent streams, the west Agulhas area in which all the rivers are small and from which no redfin minnows have been recorded, the east Agulhas area including the large Breë River and adjacent streams, and the south coastal area that includes a number of smaller rivers draining the southern flanks of the Outeniqua and Tsitsikama mountain ranges.

The Orange River system arises in the Drakensberg and Maluti Mountains and, as the Vaal sub-system, on the Transvaal and Orange Free State Highveld, to drain westward to the Atlantic Ocean. The Drakensberg Mountains rise to 3 480 m and form an escarpment of extensive sub-horizontal strata of Karoo sediments capped by thick basalts of the "Drakensberg formation" (Truswell, 1977). The source tributaries often arise from seepage bogs that provide clear, slightly acidic waters. Water quality changes rapidly once the streams reach the underlying Beaufort sediments which contribute large quantities of dissolved and suspended matter (Cambray *et al.*, 1986).

MATERIALS AND METHODS

Linear and meristic measurements

Measurements were taken with vernier calipers and recorded to the nearest 0,1 mm. The pharyngeal bones were measured using a calibrated graticule on a binocular stereo microscope. Samples included specimens of both sexes and initially the measurements were analysed separately for each sex and collectively for the sample, if no difference between the sexes was evident. As far as possible only specimens of adult proportions (i.e. > 50 mm SL) were used for the intra- and interspecific analysis. Wherever possible the samples included 30 specimens and at least one sample of each species included a broad size range of specimens to assess allometry.

Linear measurements, as shown in Fig. 2 , were taken according to Hubbs and Lagler (1958) except as follows:

(i) measurements from the anterior end of the head were taken from the anterior symphysis of the retracted premaxillae.
(ii) measurements on the head were taken from the bony margins of the reference points.
(iii) predorsal length was measured along the horizontal to the intersection of the vertical line through the anterior base of the fin.
(iv) pectoral to pelvic length is the median distance between the posterior margins of the bases of the fins.
(v) pelvic to anal length is the median distance between the posterior margin of the pelvic bases and the anterior margin of the anal fin base.
(vi) pharyngeal bones were measured according to Chu (1935) (Fig. 3). The pharyngeal bones were dissected from 10 specimens from each sample, macerated in trypsin solution for a few days and then defleshed with forceps and dried. Pharyngeal teeth were counted in rows and presented in a formula (Eastman and Underhill, 1973) giving the number on the left bone from the minor (outer) row to the major (inner) row followed by the number on the right bone, from the major (inner) to minor (outer) row.
(viii) the length of the gut (intestine) was measured according to the method of Snelson (1971). The tract was severed immediately behind the transverse septum of the body cavity and at the anus. Viscera were detached and the tract straightened and pinned to a board without stretching for measurement to the nearest 1,0 mm.

Measurements are expressed as percentage Standard length (SL) except for the following which are given as percentage head length (HL): head depth, snout length, orbit diameter, postorbit length and interorbit length. Barbels are given as percentage orbit diameter (OD).

Meristic characters are given with the number of individual specimens counted in

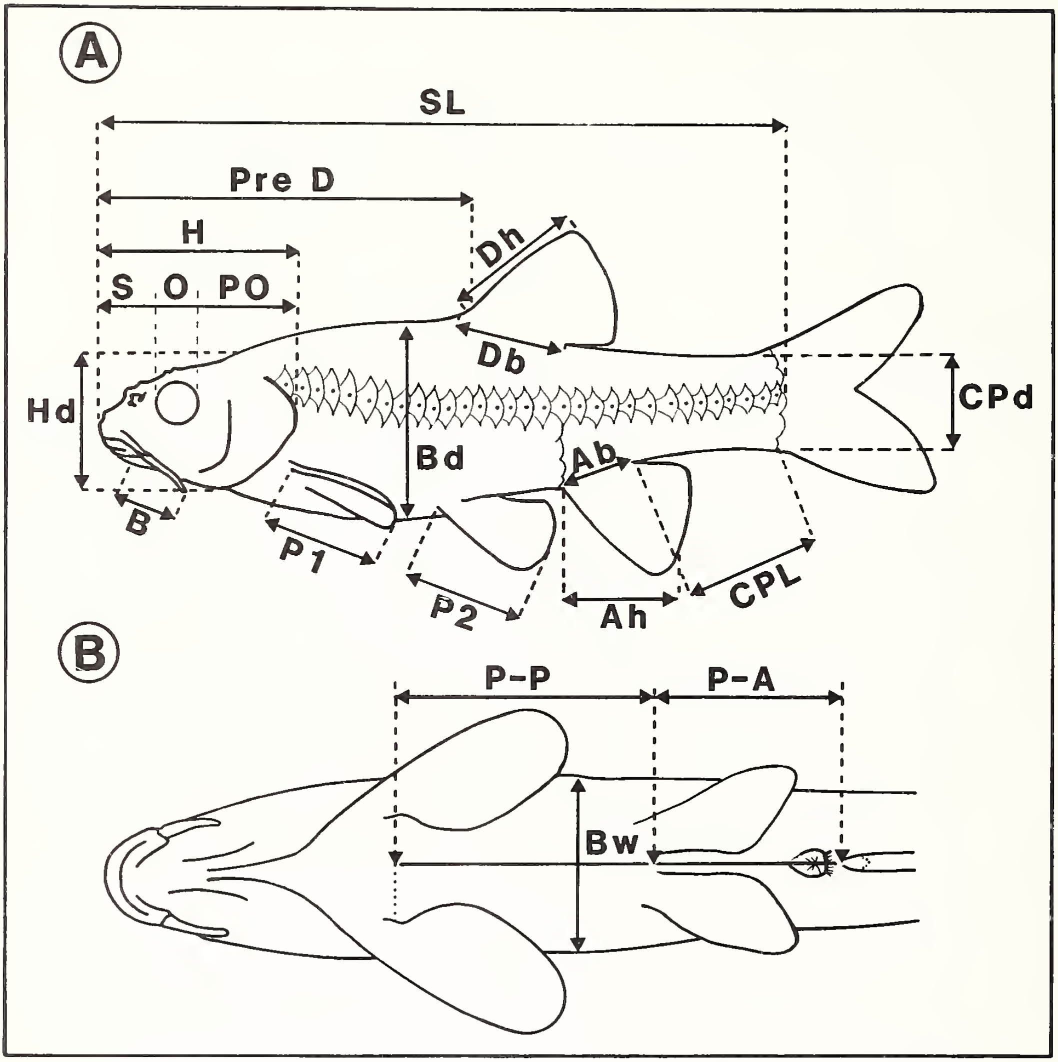

Fig. 2. Linear measurements in this study. Abbreviations : Ab—anal fin base; Ah—anal fin height; B—barbel length; Bd—body depth; Bw—body width; CPd—caudal peduncle depth ; CPL—caudal peduncle length; Db—dorsal fin base; Dh—dorsal fin height; HL—head length; Hd—head depth; O—orbit diameter; P1—pectoral fin length; P2—pelvic fin length; PO—postorbit length; P-A—pelvic to anal fin length; P-P—pectoral to pelvic fin length; PreD—predorsal length; S—snout length; SL—standard length.

parenthesis. Scale and fin ray counts were made as in Hubbs and Lagler (1958) (Fig. 4a) except for the predorsal scale count which was taken as in Snelson (1972). This count records the number of oblique scale rows crossing an imaginary line between the anterior base of the dorsal

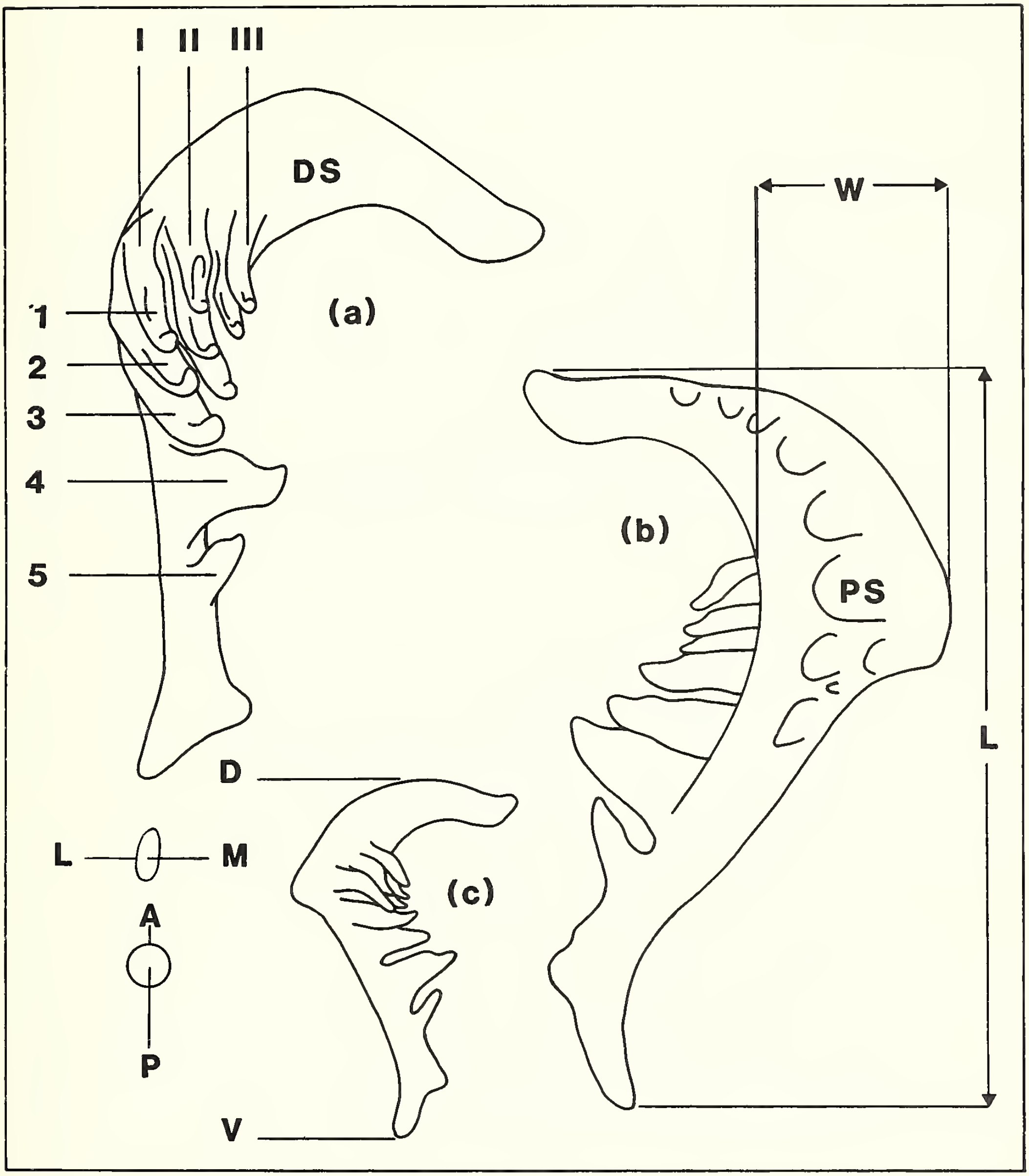

Fig. 3. Measurements and orientation of pharyngeal bones. (a) postero-medial view of the left pharyngeal bone: I—major or inner row, II—middle row, III—minor or outer row. (b) antero-lateral view of left pharyngeal bone : L—length, W—width. (c) orientation : A—anterior, D—dorsal, V—ventral, M—medial, PS—pitted surface, DS—dorsal surfaee.

fin and the posterior margin of the head at the nape. Single scales interposed between two otherwise regular rows are omitted.

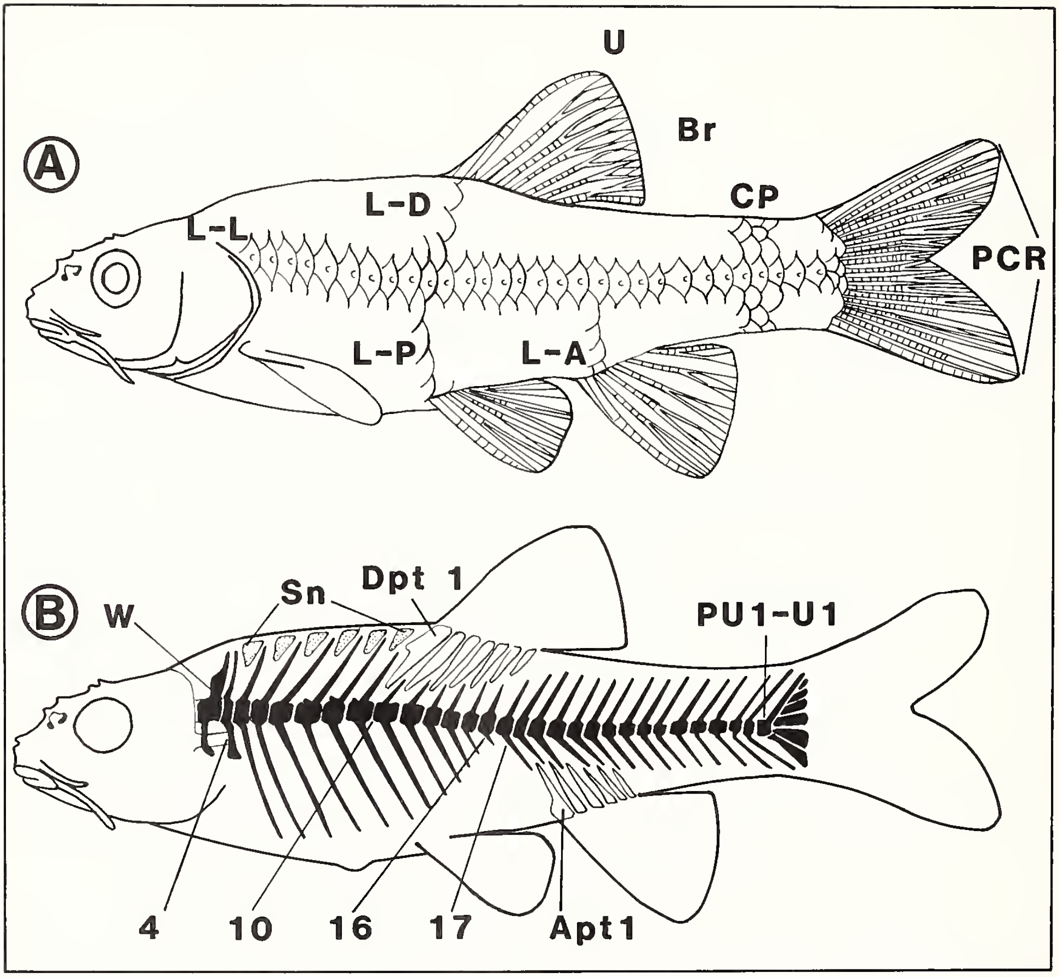

Fig. 4. Meristic measurements as taken in this study. (a) scale and fin ray counts, (b) post-cranial skeletal meristics. Apt1—first anal pterygiophore, Br—branched fin rays, CP—caudal peduncle scale rows, Dpt1—first dorsal fin pterygiophore, L-A—lateral line to anal fin scale rows, L-L—lateral line scales, L-P lateral line to pelvic fin scale rows, PCR—principal caudal fin rays, PU1+U1—compound ural centrum, Sn—supraneural bones, U—unbranched fin rays, W—Weberian vertebrae, 4–4th vertebra, 10—last predorsal vertebra, 16—first caudal vertebra, 17—last preanal vertebra.

Branched and unbranched rays are considered separately in the case of the dorsal and anal fins, but all rays are included in a single count in the case of the pectoral and pelvic fins. Principal

caudal rays were counted as branched rays plus a single outer dorsal and ventral unbranched or simple ray.

Postcranial skeletal meristics were taken from radiographs as shown in Fig. 4b. Vertebral counts include the four Weberian vertebrae and a single ural centrum (PU1 + U1). The first caudal vertebra was taken as the first unit with a closed haemal arch as indicated by a bright exposure point on the radiograph (an indication of increased bone density). Vertebrae before the dorsal (predorsal vertebrae) or anal fins (preanal vertebrae) include all vertebrae before or opposite the respective leading pterygiophore. Supraneural bones include all independent bones between the head and the first dorsal pterygiophore.

The number of scale radii is the mean number of radii counted from five scales, each scale taken from one of the following different body regions on the right side: above and below the lateral line in the area before the dorsal fin, and behind the dorsal fin above and below the lateral line. Scales were removed, stained in alizarin red, defleshed and examined under a stereo microscope. Primary radii were considered as radii extending from the focus to or close to the scale margin. Scales with a diffuse focus were excluded from the count.

Osteology

Specimens were cleared with trypsin and stained for bone with alizarin red (Taylor, 1967). The study was completed before the double cartilage-bone staining methods using alcian blue for cartilage were available. Cartilage components were therefore stained with Victoria blue after dissection of a particular skeletal complex.

Phylogenetic analysis

The full results of the phylogenetic analysis are being prepared for separate publication (Skelton, in prep. a). At a generic level the phylogenetic relationships have been incorporated into this paper and the methods employed in the analysis are therefore presented here. Species interrelationships were investigated in accordance with the philosophy of cladistics or phylogenetic systematics (Wiley, 1981). The original phylogenetic methods of Hennig (1950 and 1966) included a number of principles and practices of which all but one have been discarded as a means of determining the phylogenetic relationships between taxa. The valid criterion is that related taxa share at least one relatively derived (homologous) character state (synapomorphy) which is not shared with other taxa. A monophyletic group is considered to be one which includes a common ancestor and all of its descendants (Wiley, 1981).

Character state was determined according to the method of out-group comparison (Wiley, 1981). The operating principle behind the method is given by Wiley (1981) as the 'out-group rule' as follows: given two characters that are homologues and found within a single monophyletic group the character that is also found in the sister group is the plesiomorph (less derived or primitive state) whereas the character found only within the monophyletic group is the apomorphic character. A complementary method of character state evaluation is one using the ontogenetic criterion which is stated by Wiley (1981) as : "given an ontogenetic character sequence which goes from a character found in the outgroup to a character found only within the group considered, the character found only in the group considered is the derived character and the character found in the out-group is primitive."

Abbreviations

Institutional abbreviations follow Leviton *et al.* (1985) and are: AMGP—Albany Museum, Grahamstown (fish collection); BMNH—British Museum (Natural History), London; MRAC

—Musee de l'Afrique Centrale, Tervuren; MNHN—Museum National d'Histoire Naturelle, Paris; NMP—Natal Museum, Pietermaritzburg; RUSI—J. L. B. Smith Institute of Ichthyology, Grahamstown; SAM—South African Museum, Cape Town; TMP—Transvaal Museum, Pretoria.

Character and osteological abbreviations are: Ab—anal fin base; Ah—anal fin length; Apt—anal pterygiophore; B—barbel length; Bd—body depth; Br—branched rays; Bw—body width; CP—caudal peduncle scale rows; CPd–caudal peduncle depth; CPL—caudal peduncle length; Db—dorsal fin base; Dh—dorsal fin height (length); Dpt—dorsal pterygiophore; H—head length; Hd—head depth; L-A—lateral line to anal fin scale rows; L-D—lateral line to dorsal fin scale rows; LL—lateral line scales; L-P—lateral line to pelvic scales; O—orbit diameter; PCR—principal caudal rays; PL—pectoral fin length; P2—pelvic fin length; PO—postorbit length; P-A—pelvic to anal fin length; P-P—pectoral to pelvic fin length; Pre D—predorsal length; Pu1+U1—compound ural vertebral centrum; S—snout length; SL—Standard length; Sn—supraneural bone(s); U—unbranched fin rays; W—Weberian vertebrae (vertebrae 1–4).

Materials

All redfin material used in this study is recorded under the individual species accounts. The samples used for morphometric and meristic measurements are given in Table 1 and their respective localities are shown in Fig. 5.

Table 1.

Samples of redfin minnows measured.

Species	Collection No.	Locality No. (Fig. 5)
B. burchelli	AMG/P 1411, 3463	23
	AMG/P 2079	19
	AMG/P 2077	20
	AMG/P 3472	18
	AMG/P 1368	24
	AMG/P 1566	21
	SAM 18731	22
B. burgi	AMG/P 2076, 1578	27
	AMG/P 1874, 1875	28
	SAM 18747	26
	SAM 4695, 5090	25
	BMNH 1901.2.11:14–16	27
	SAM 4696	27
B. phlegethon	SAM 22484	29
	SAM 22749	29
	SAM 22483	29
	AMG/P 722	30
	AMG/P 1394	29
	AMG/P 1852	32

Species	Collection No.	Locality No. (Fig. 5)
	AMG/P 1863	30
	AMG/P 2054	35
B. tenuis	AMG/P 2081, 1935, 608	(not plotted)
	AMG/P 2666	15
	AMG/P 2667	16
	AMG/P 3186	11
B. afer	AMG/P 609	1
	AMG/P 745, 2524	2
	AMG/P 766	3
	AMG/P 2651	8
B. afer (Gamtoos)	AMG/P 1415	4
	AMG/P 1374, 1375	5
	AMG/P 1921	6
B. asper (variant)	AMG/P 2652, 2654	9
	AMG/P 2656	9
	AMG/P 2659	10
	AMG/P 1790	11
	AMG/P 110, 584	11
B. asper	AMG/P 1744	7
	AMG/P 2663	13
	AMG/P 1699	17
	AMG/P 607	14
B. calidus	AMG/P 1871	29
	AMG/P 1862	30
	AMG/P 1797, 1371	31
	AMG/P 1850	32
	AMG/P 1844	33
	AMG/P 1855	34
	AMG/P 1857	34
B. erubescens	AMG/P 1867, 2045, 2049	36
	AMG/P 1866, 2075	36
	AMG/P 2074	36
O. quathlambae	AMG/P 1540, 1877, 1823	37
	AMG/P 3473–3478	37
	AMG/P 3479	38
	AMG/P 3480	39
	SAM 19018	40

Delimitation of taxa for analysis

A preliminary analysis of the results of the morphometric and meristic characters was made according to the individual samples (populations) measured as in Table 1. The species to which these samples were assigned are those established by Jubb (1965 and 1967), Barnard (1938a) and Skelton (1974b). In the case of *Barbus afer* and *B. asper* there was some doubt as to which of the species certain of the samples should be referred. These samples were therefore analysed separately and labelled as *B. asper* (variant) and *B. afer* (Gamtoos). *B. asper* (variant) refers to the populations of redfins found in the coastal streams between the mouth of the Gourits and the

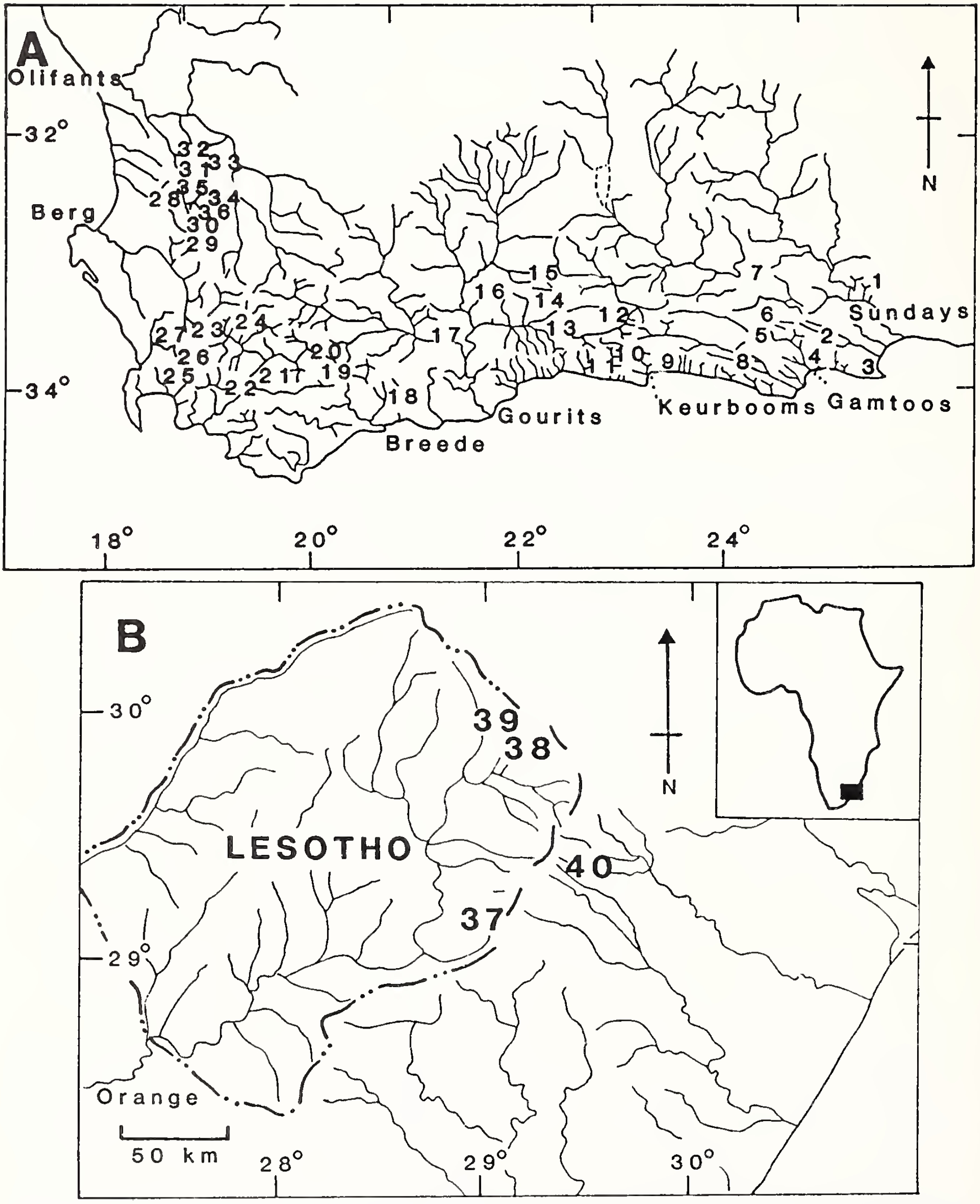

Fig. 5. Localities of samples used for morphometric and meristic analysis (a) south coastal drainages (b) upper Orange and adjacent river drainages. Localities as given in Table 1.

mouth of the Gamtoos except for the Kromme River population which was included in *B. afer* (Jubb, 1965). Populations of redfins from the Fold Mountain tributaries of the Gamtoos River system are those referred to *B. afer* (Gamtoos). Typical *B. asper* also occurs in the Gamtoos River system but this species was found to be restricted to the large Groot River tributary of this system.

As this investigation progressed it became evident that the major character differences lay between *B. calidus* and *B. erubescens* on the one hand, and the remaining species on the other. To facilitate repetitive reference to these groups they are named the "serrated" and "flexible" rayed species respectively (in reference to the nature of their last unbranched dorsal fin ray).

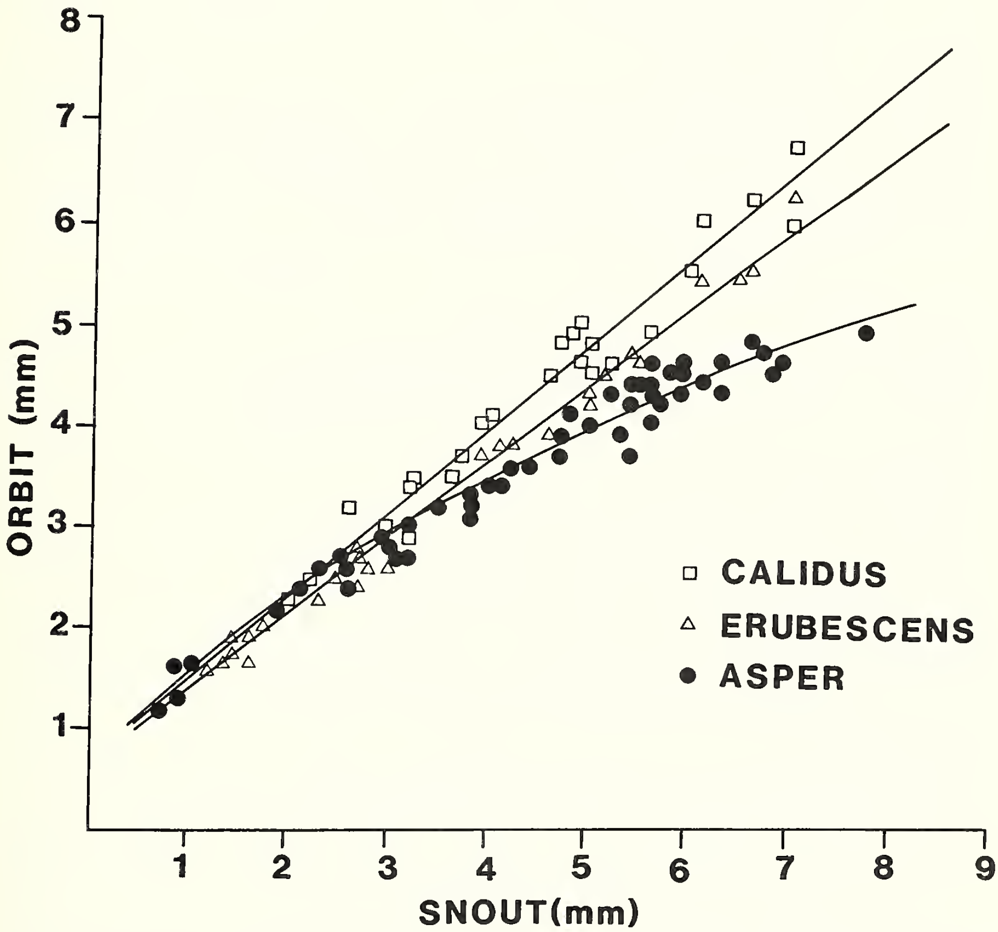

Fig. 6. The relationship between orbit diameter and length of the snout in three redfin minnows *B. asper*, *B. calidus* and *B. erubescens*.

CHARACTER ANALYSIS

Linear measurements

The morphometric measurements for each species are given under the individual descriptive accounts (Tables 14–22). The species are generally similar in form so that many measurements differ only slightly between them and are therefore mainly useful for the purpose of description. Only measurements or proportions which serve to distinguish a species or exhibit noteworthy intraspecific variation will be elaborated on in this section.

The largest redfin specimen examined was a *B. burchelli* of 134 mm SL. Gephard (1978) reports a specimen of *O. quathlambae* of 143 mm total length (TL) which is also about 130 mm SL. The largest specimen of *B. phlegethon* measured 71 mm SL making it the smallest redfin species. The maximum size for the other redfin species lies between 85 mm SL (*B. tenuis*) and 120 mm SL (*B. burgi*).

Of the head proportions the ratio between the snout length and the orbit diameter establishes an interesting difference between the two "serrated" species and the "flexible" species (Fig. 6). In *B. calidus* and *B. erubescens* the plot of orbit diameter against snout length is linear but in the flexible rayed species (e.g. *B. asper* in Fig. 6) a curvilinear function is described and the orbit is relatively smaller in larger specimens.

The depth of the head is least in *O. quathlambae* and *B. tenuis* and both species have a more slender body profile (depth) than other redfins (Fig. 7).

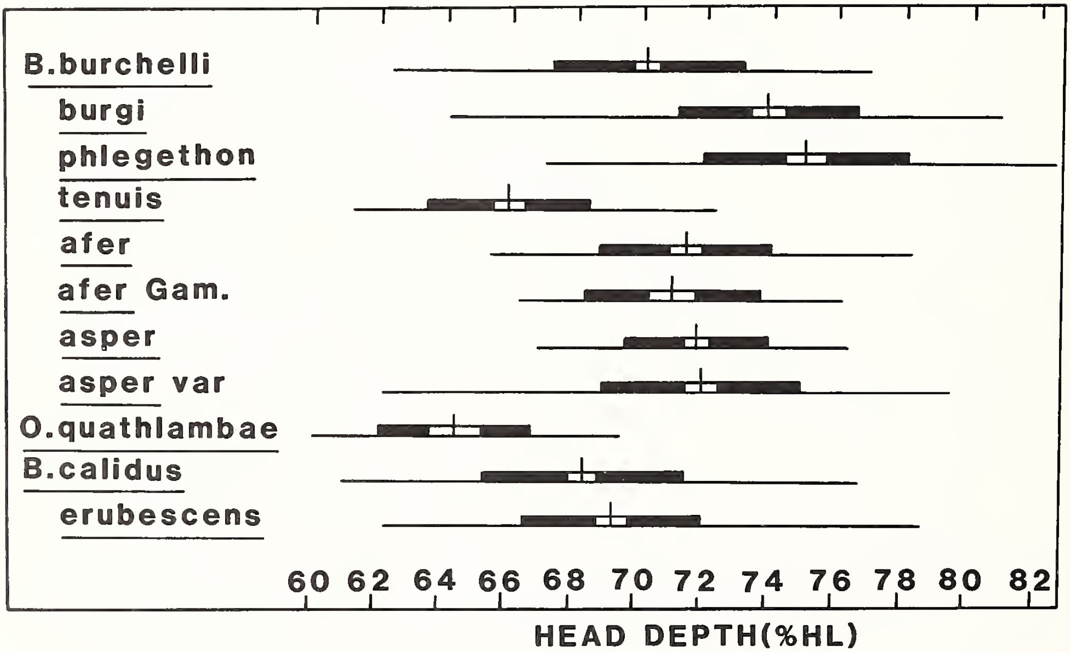

Fig. 7. Head depth (%HL) of redfin minnows.

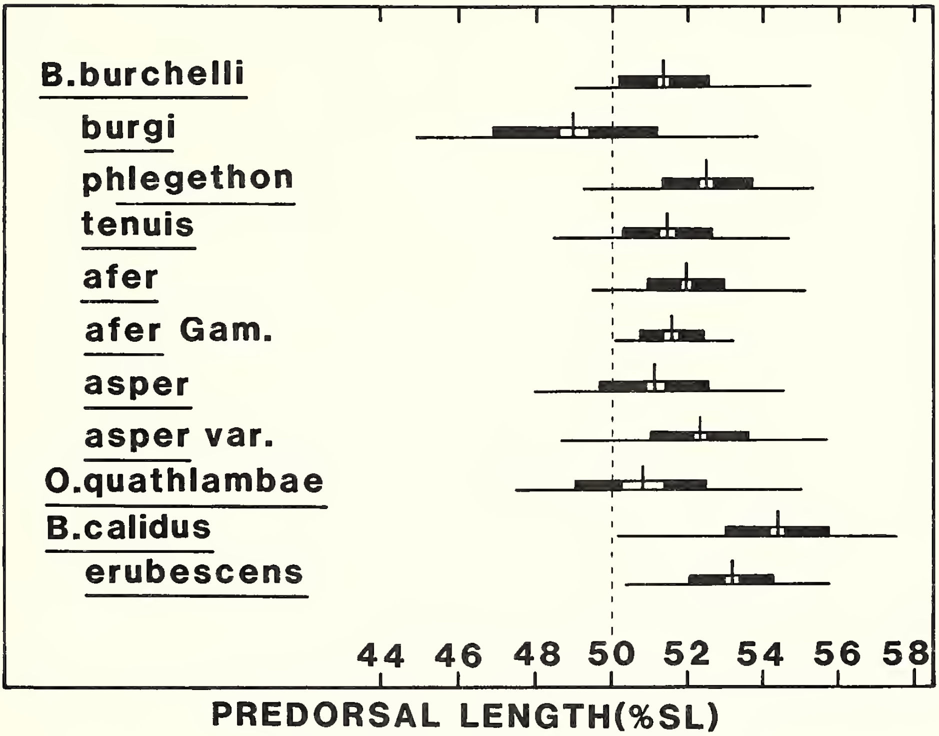

Fig. 8. Predorsal length (%SL) of redfin minnows.

The results of the analysis of the predorsal length include two pertinent taxonomic features *viz.*, *B. burgi* has a relatively short predorsal length and *B. calidus* and *B. erubescens* have relatively longer predorsal lengths than the other redfins (Fig. 8). In the case of *B. burgi* there is, however, a considerable amount of intraspecific variation in this character and it is only in the Berg River samples that the predorsal is shorter than in other redfin species. The shorter predorsal length in *B. burgi* correlates with a shorter head length in Berg River specimens (Fig. 9). It appears that this may account for the phenomenon but it is also noted that *B. burgi* has the lowest modal predorsal vertebral count (Table 6) which would also tend to reduce the predorsal length.

A relatively high predorsal vertebral count in *B. calidus* may likewise account for the long predorsal length of the species (Fig. 8 and Table 6D). The origin of the dorsal fin in both *B. calidus* and *B. erubescens* is placed behind the vertical through the origin of the pelvic fins whereas in the other redfin species the dorsal fin origin lies over or only slightly behind the origin of the pelvics.

Barnard (1943) distinguished *B. tenuis* from *B. asper* and *B. afer* on the basis of body depth. Body depth is generally an unreliable cyprinid taxonomic character because it is so easily influenced by the condition of the specimen both in the living and preserved states. In spite of these limitations the redfin species do have fairly characteristic profiles and it is useful to note

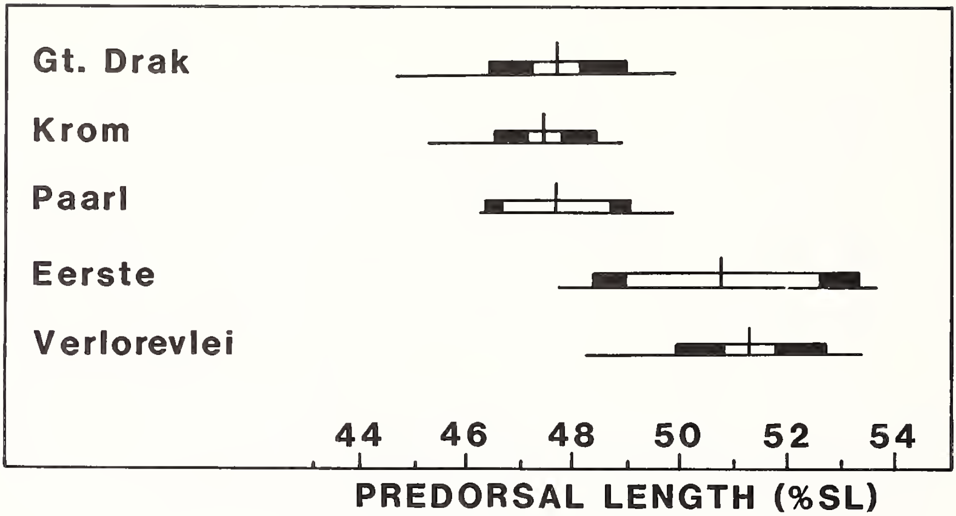

Fig. 9. Intraspecific variation in the predorsal length of *B. burgi*.

that the body depth in these minnows correlates generally with the length of the intestine. The redfins form two fairly distinct groups with regard to body depth, those with a slender profile—*B. tenuis*, *O. quathlambae*, *B. calidus* and *B. erubescens*, and the rest with relatively deep body profiles (Fig. 10). The former species with shallow profiles all have relatively short guts (see below, p. 243) and the deeper bodied forms have longer more involuted intestines.

Some interesting trends are evident in the proportions of the caudal peduncle of redfin species. The peduncle of *B. calidus* and *B. erubescens* is shorter than in the flexible rayed species (Fig. 11). Intraspecific variation in this character is not usually marked but an exception is in *B. asper* where the specimens from the Gamtoos River system have a significantly longer caudal peduncle than those from the Gourits River system (Fig. 12). There is a tendency for the males of flexible rayed redfins to have slightly deeper caudal peduncles than do females (Fig. 13). *B. calidus* has a relatively narrow caudal peduncle, and this is taxonomically useful in comparison with *B. erubescens*.

Barbels are frequently employed as taxonomic characters in cyprinids and although their value is often overestimated (Gilbert and Bailey, 1972, and Schmidt, 1983), when used in the correct context and perspective, they may be extremely useful features. The redfins have either one or two pairs of simple barbels. The posterior pair is characteristic of all the species but an anterior pair is consistently present only in *B. burchelli*, *B. burgi*, *B. calidus* and *B. erubescens* (Fig. 14). Occasionally individual specimens of the other species have one or two anterior barbels. Certain populations of *B. tenuis* have a fairly high incidence of anterior barbels, e.g. 20% of the specimens from the Waterkloof River (Gourits system) had anterior barbels, but 50% of these had only a single anterior barbel.

The anterior barbels of *B. burgi* develop relatively late and are visible in specimens greater than about 45 mm SL (Barnard, 1943). In *B. burchelli* these barbels develop at an earlier stage and are therefore longer than those of similar sized *B. burgi*. Short barbels are characteristic of

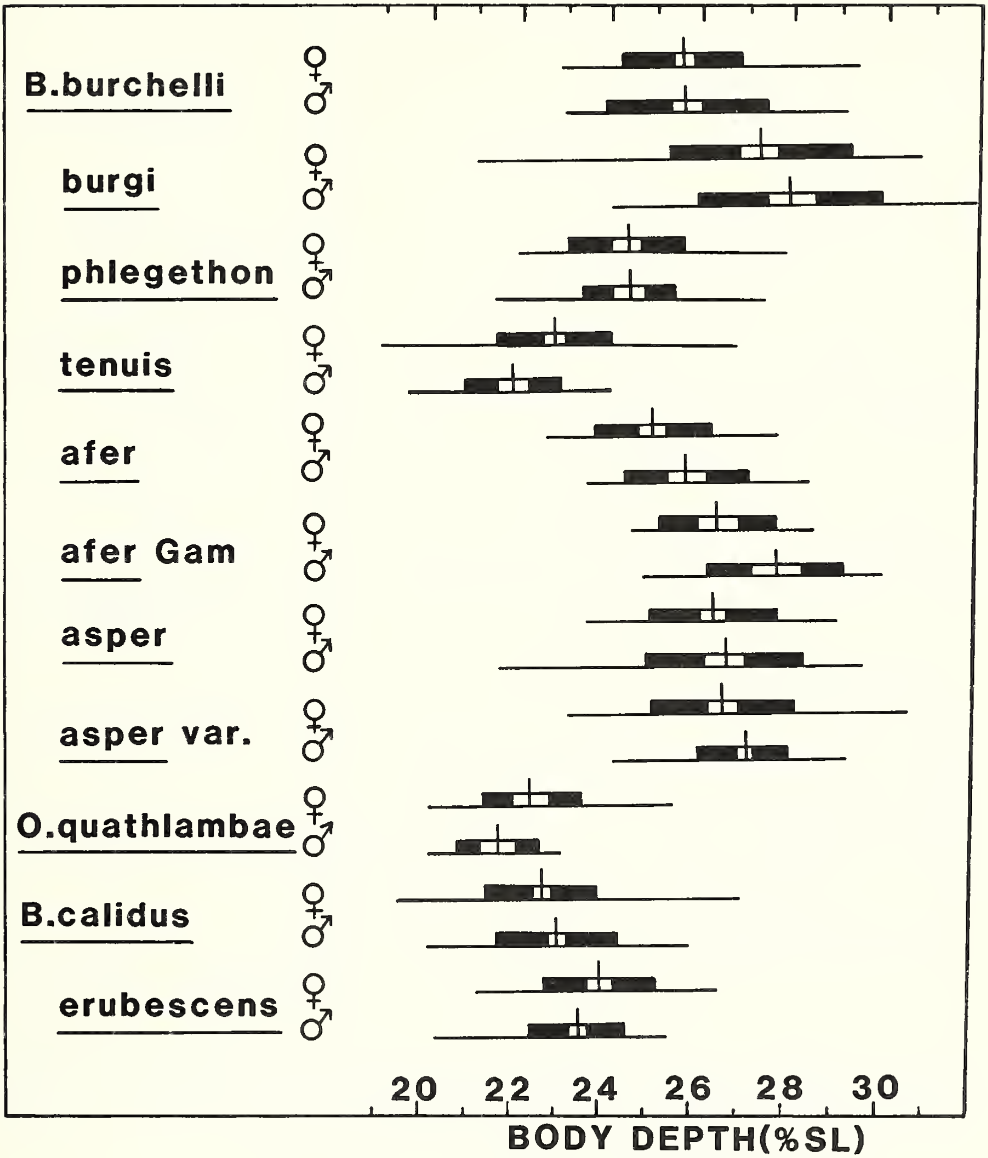

Fig. 10. Body depth (%SL) of redfin minnows.

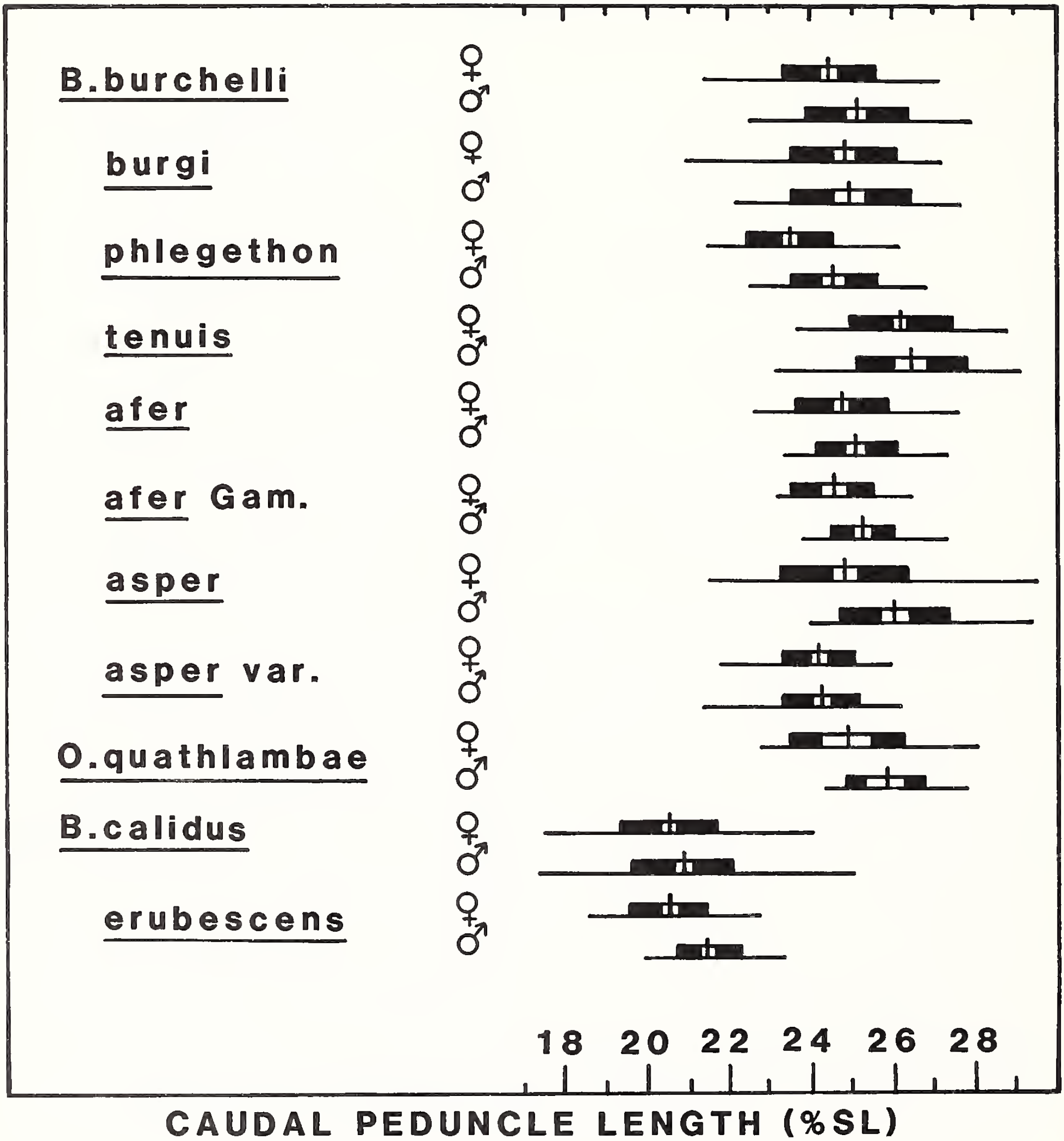

Fig. 11. Caudal peduncle length (%SL) of redfin minnows.

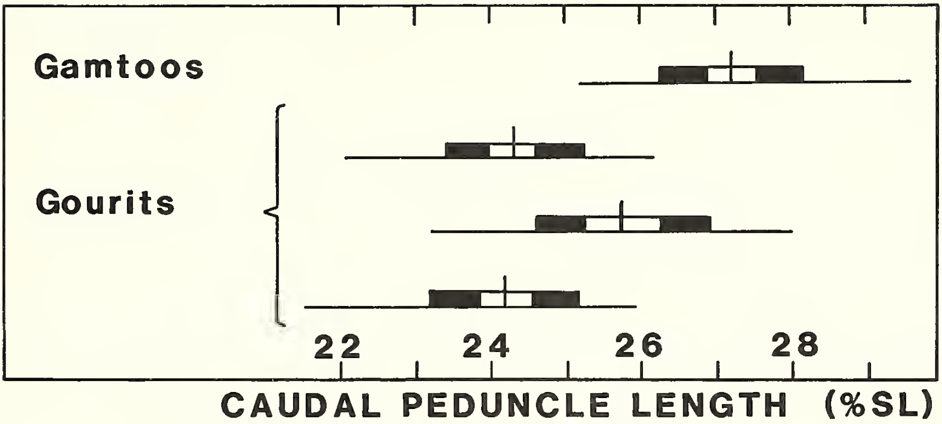

Fig. 12. Caudal peduncle length (%SL) of *B. asper*.

B. phlegethon and *O. quathlambae* (Fig. 14). The actual length of the barbels is subject to considerable intraspecific variation especially in the widespread species such as *B. afer* and *B. asper* (variant) populations.

Fins

The fins of cyprinid fishes are well known to be labile structures with their shape and proportions subject to the environmental and functional demands placed on them (Hubbs, 1940 and Alexander, 1967). There are no outstanding taxonomic differences between the length of the fins of redfin species. Intraspecific differences are in certain cases at least as large as interspecific differences. In *B. tenuis* for example the population from the Keurbooms River system has relatively longer fins than conspecifics in the Gourits River system. The Keurbooms catchment receives a higher mean average rainfall compared to Gourits River catchments (Midgeley and Pitman, 1969). This suggests that flow is likely to be higher on average in the Keurbooms, a factor which favours the development of longer fins (Hubbs, 1940) and may be responsible for the observed differences in this case.

Sexual dimorphism of the fins is clearly evident in most of the flexible-rayed species (Barnard, 1943). Boulenger (1911) indicated that the pectoral fins of *B. asper* males were longer than those of the females. Barnard (1943) qualified this statement of dimorphism by referring to the length of the pectoral relative to the base of the pelvic fins. In males of the flexible-rayed species the pectorals reach the base of the pelvics but in the females the pectorals are short of the pelvics. In the case of juveniles the pectoral fins reach the pelvics (except in *B. phlegethon*).

The length of the pectoral and the pectoral to pelvic distance is shown in Fig. 15. Apart from *B. calidus* and *B. erubescens* the males have relatively longer pectoral fins but shorter distances between the fins than the females. Interspecific differences and differences between the sexes in the shape of the pectoral fins are evident from Fig. 16. The males have generally broader more rounded fins than the females.

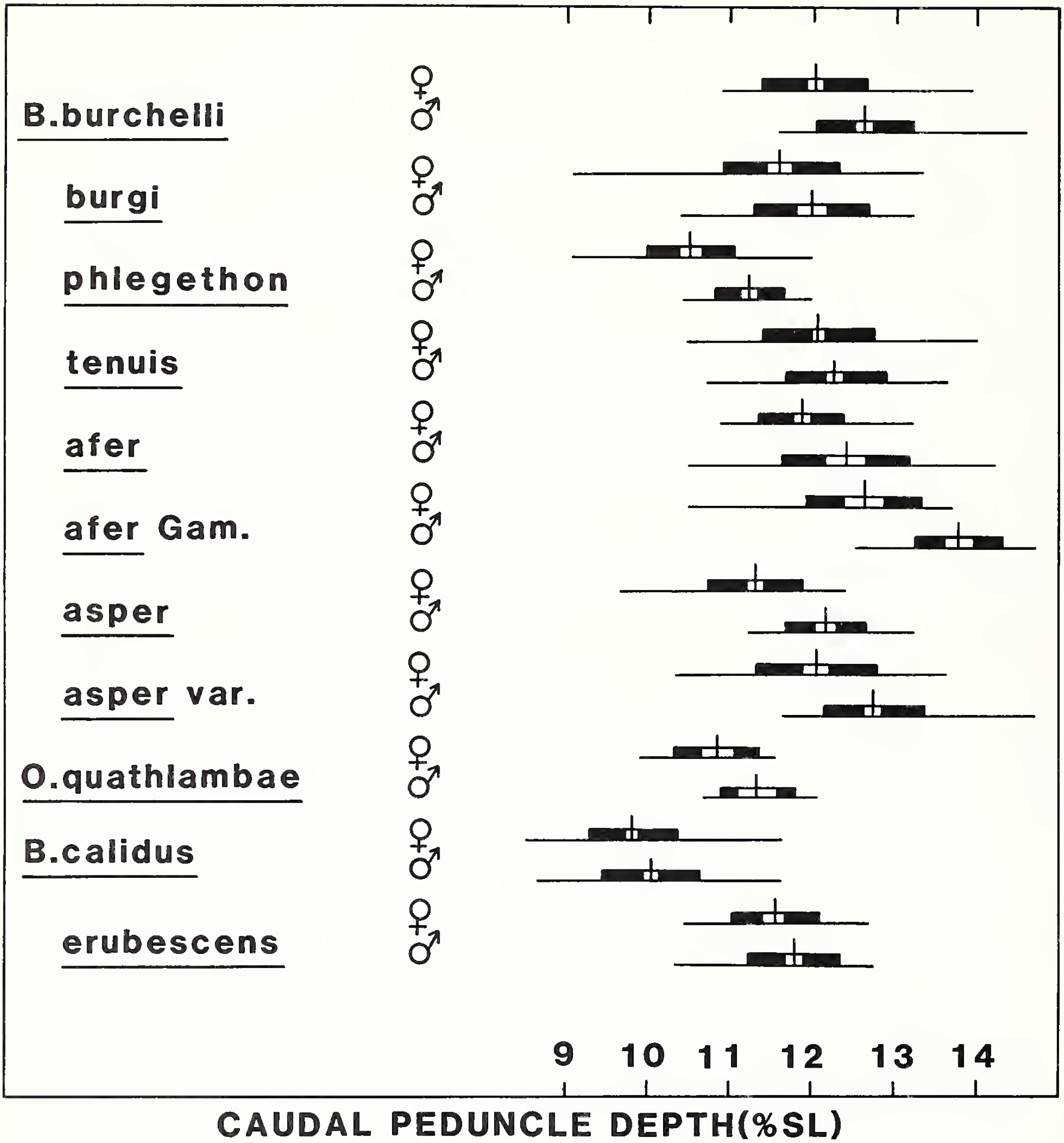

Fig. 13. Caudal peduncle depth (%SL) of redfin minnows.

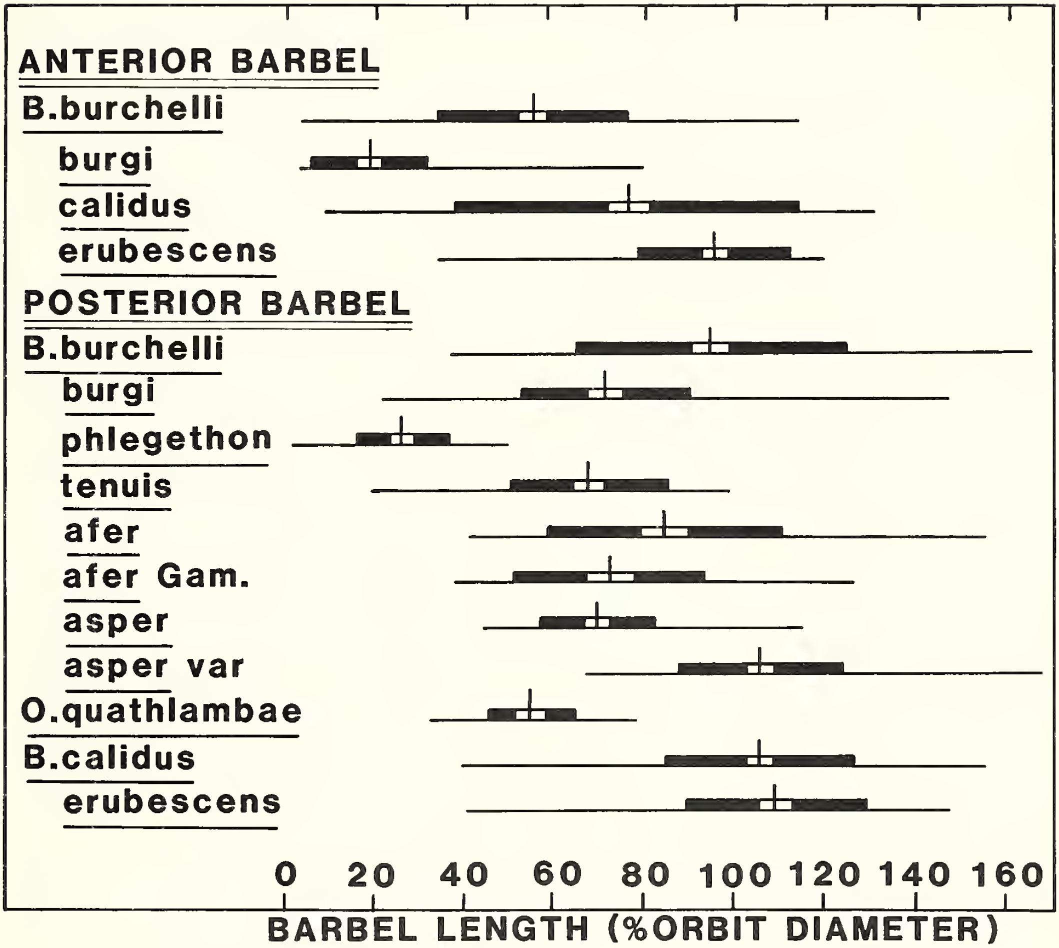

Fig. 14. The length of the anterior barbel and the posterior barbel (% Orbit diameter) of redfin minnows.

Meristics

(A) Fin rays

The number of fin rays in the dorsal, anal, pectoral and pelvic fins of redfin species are given in Table 2. In the dorsal and anal fins the number of unbranched rays is always difficult to determine accurately because the first one or two rays are very small and hidden from view. The form of the last unbranched ray in the dorsal fin is a useful character in *Barbus* (e.g. Boulenger, 1911) and is a prominent feature separating *B. calidus* and to a lesser extent *B. erubescens* from the other redfin species (Fig. 17). In *B. calidus* this ray is bony and serrated behind with only the tip being segmented and flexible. This ray is more flexible with a few reduced serrations in *B. erubescens*, and slender and flexible without serrations in all other redfin species.

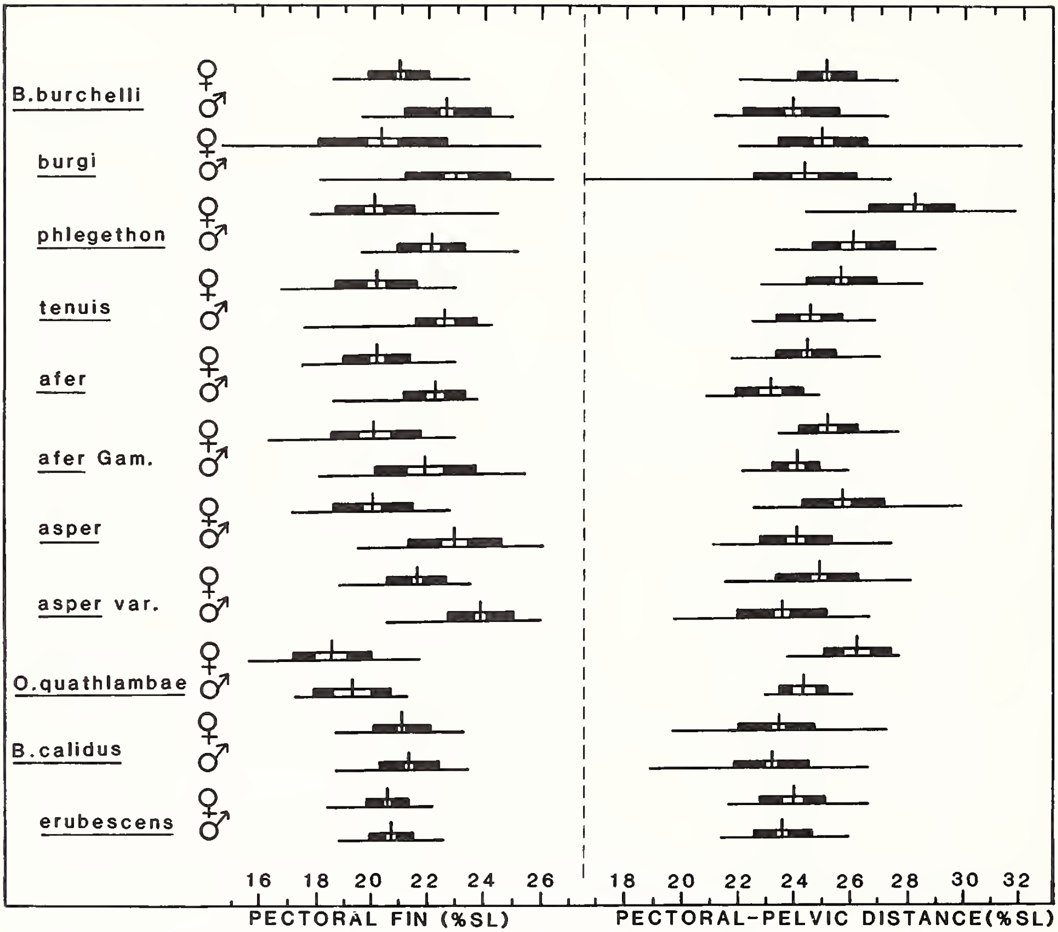

Fig. 15. The length of the pectoral fin and the pectoral to pelvic fin distance (%SL) of male and female redfin minnows.

Apart from *B. erubescens*, for which the modal number is eight, the redfins usually have seven branched dorsal fin rays (Table 2B). Similarly the majority of species have only fivebranched rays in the anal fin but this serves to emphasise the taxonomic significance of the modal six for *B. calidus* and seven for *B. erubescens* (Table 2D).

Pectoral and pelvic fin rays are seldom reported for African cyprinid species. The intraspecific range of variation in pectoral fin rays is broad which tends to diminish the value of any modal differences between the species (Table 2E). The same is true of the number of pelvic fin rays where all but *B. tenuis* have a mode of eight rays (Table 2F). The redfins have invariably 10 + 9 principal caudal fin rays.

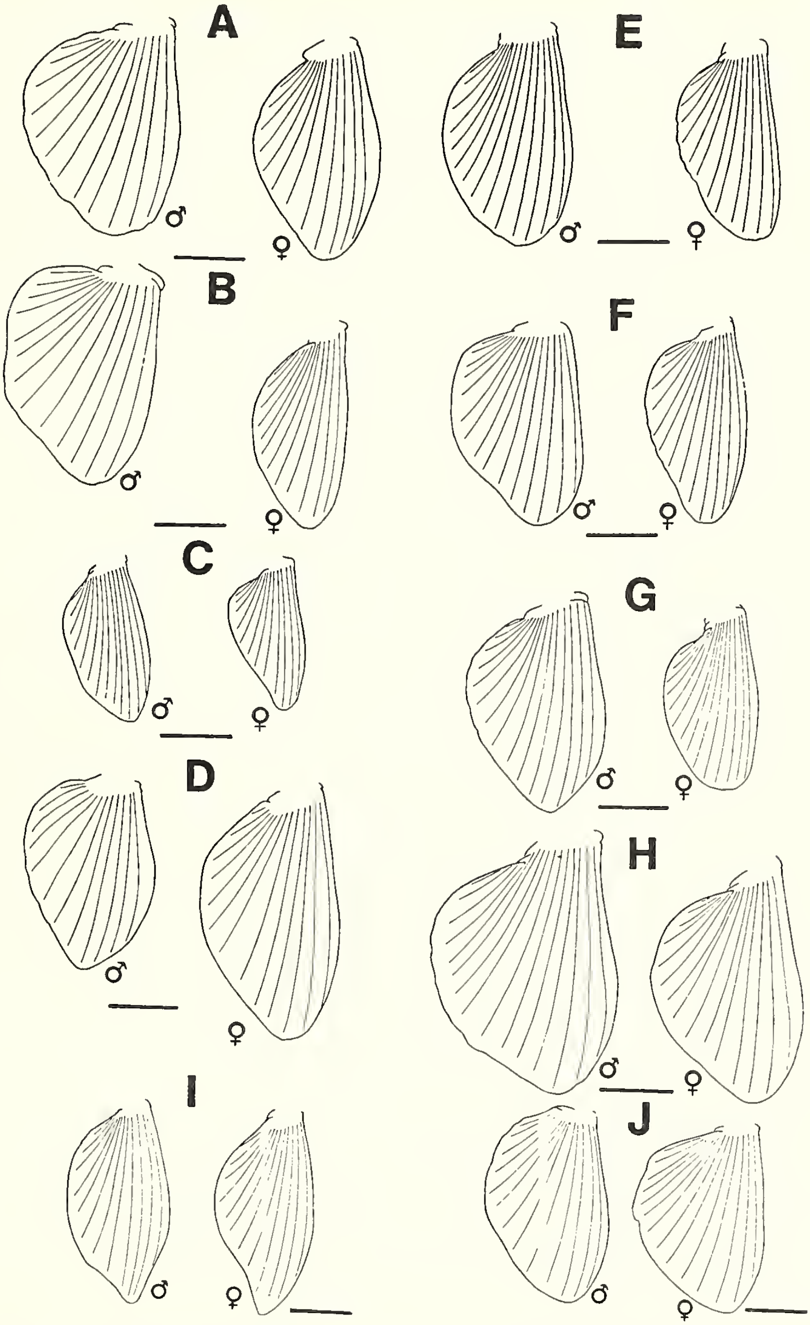

Fig. 16. Pectoral fin profiles of redfin minnows, dorsal view, right side. Scale bar = 5 mm. A. *B. burchelli*, B. *B. burgi*, C. *B. phlegethon*, D. *B. tenuis*, E. *B. afer*, F. *B. asper*, G. *B. asper* (variant), H. *O. quathlambae*, I. *B. calidus*, J. *B. erubescens*.

TABLE 2.

Fin ray counts for redfin minnows.

		A. Unbranched dorsal fin rays		B. Branched dorsal fin rays			C Unbranched anal fin rays			D. Branched anal fin rays				
Species/ (Group)	N	3	4	6	7	8	2	3	4	4	5	6	7	8
B. burchelli	179	74	105	8	166	5		130	49	1	171	7		
B. burgi	107	93	14	3	102	2	1	103	2		104	2		
B. phlegethon	90	63	27	4	85	1		85	5		89	1		
B. tenuis	96	69	27	6	88	2		90	6		93	3		
B. afer	105	37	68	2	103			105			104	1		
B. afer (Gamtoos)	50	14	36		50			48	2		49	1		
B. asper	110	11	99	5	104	1		95	15		109	1		
B. asper (variant)	142	54	88	5	133	4		137	5		142			
O. quathlambae	39	39		1	37	1		39			35	4		
B. calidus	300	10	290	1	287	12		280	20		2	278	20	
B. erubescens	110	33	77		27	83	1	107	2			7	96	7

		E. *Pectoral fin rays*								F. *Pelvic fin rays*		
Species (Group)	N	11	12	13	14	15	16	17	18	7	8	9
B. burchelli	179		1	40	90	44	4			7	160	13
B. burgi	107			4	46	42	12	2	1	1	80	26
B. phlegethon	90	1	4	36	42	7				11	78	1
B. tenuis	96		4	30	48	13	1			70	26	
B. afer	105			5	29	41	25	5			98	7
B. afer (Gamtoos)	50				4	29	12	5		2	46	2
B. asper	110				7	48	43	12		4	86	20
B. asper (variant)	142			9	41	68	22	2		8	123	11
O. quathlambae	38					8	21	9		4	31	3
B. calidus	280	1	10	141	116	12				28	237	15
B. erubescens	110	1		5	62	41	1			14	96	

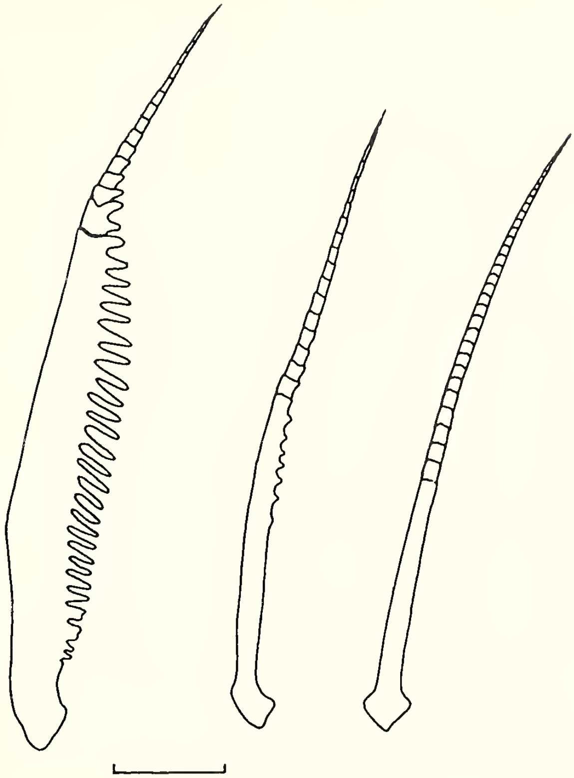

Fig. 17. The form of the last unbranched ray of the dorsal fin of redfin minnows. A. *B. calidus*, B. *B. erubescens*, C. *B. afer*.

(B) Scale counts.

Distribution frequencies of the various scale counts for redfin species are given in Table 3. There is a wide range of variation in the counts and only two species are really distinctive in the group on account of the size of their scales. These two species are *O. quathlambae*, which has exceptionally small scales, and *B. asper*, which also has relatively small scales.

Scale size, as assessed by scale counts, is an important factor in the problem of delimiting the two species *B. asper* and *B. afer*. The distribution frequencies of the lateral line counts of the different populations of the two species and their "variant" groups are given in Table 4 with graphic summaries in Fig. 18. A wide range of counts is characteristic of most of the samples. *B. afer* samples indicate a low mode of about 32 with the exception of the Kromme River sample where the mode is 29. In the Gamtoos system *B. afer* samples have a mode of 36 and those of *B. asper* 37. *B. asper* (variant) samples show a mode of 34 or 35 lateral line scales.

The summaries of lateral line counts for these samples depicted in Fig. 18 provide four taxonomic options. Firstly all the populations can be considered to be of a single polytypic species (Fig. 18A). Although the distribution curve is normal for this option the range of

TABLE 3.

The frequency distribution of the number of scales or scale rows in redfin species.

		A. *Lateral line scales*																					B. *Lateral line to dorsal fin scale rows*										
Species (Group)	N	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	4	5	6	7	8	9	10	11	12	13	14
B. burchelli	179					2	4	7	10	18	32	51	33	15	6	1								28	133	18							
B. burgi	107				2	4	14	17	23	19	14	9	4	1									6	66	35								
B. phlegethon	90					1			7	7	19	40	14	2									33	56	1								
B. tenuis	96								2	8	14	36	30	6									3	86	7								
B. afer	105	1	2	3	4	12	14	11	24	11	16	5	1	1									16	70	19								
B. afer (Gamtoos)	50										2	11	22	15										6	43	1							
B. asper	110											1	10	26	24	17	15	11	2	1	2	1			4	65	37	4					
B. asper (variant)	142					2	1	6	12	27	34	38	20	1	1									41	101								
*O. quathlambae**	34																												4	16	13		1
B. calidus	283										2	13	67	124	69	8								60	220	3							
B. erubescens	110											2	6	50	45	6	1							38	72								
		60	61	62	63	64	65	66	67	68	69	70	71	72																			
**O. quathlambae*	34	1	2	1	1	4	5	6	5	3	5			1																			

		C. *Caudal peduncle scale rows*															D. *Lateral line to pelvic fin scale rows*									
Species (Group)	N	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	3	4	5	6	7	8	9	10	11	12
B. burchelli	179			92	23	23	17	20	3	1								122	53	4						
B. burgi	107			98	4	4		1									2	76	29							
B. phlegethon	90	1	6	65	15	3											24	66								
B. tenuis	96		1	51	19	18	4	3									20	73	3							
B. afer	105	1	10	45	10	16	15	8									15	87	3							
B. afer (Gamtoos)	50					1	7	41	1									10	39	1						
B. asper	110							7	2	20	25	46	3	7					15	65	26	4				
B. asper (variant)	142			2	5	25	33	76		1							1	89	52							
*O. quathlambae**	34																					2	7	14	9	2
B. calidus	283			33	31	78	51	86	4								217	64								
B. erubescens	110						26	58	22	3	1						8	100	2							
		30	31	32	33	34	35	36	37	38																
**O. quathlambae*	34	1		8	5	6	4	7	2	1																

		E. *Predorsal scale rows*															F. *Lateral line to anal fin scale rows*								
Species (Group)	N	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	3	4	5	6	7	8	9	10	11
B. burchelli	176			2	13	23	49	40	35	7	4	3						105	72	2					
B. burgi	107	5	18	21	43	12	5	3									3	98	6						
B. phlegethon	90			1	8	21	34	15	10	1							43	46	1						
B. tenuis	96			1	8	35	15	11	5	13	7	1					6	89	1						
B. afer	105		2	27	49	23	4										20	81	4						
B. afer (Gamtoos)	50			1	5	21	11	5	6									11	39						
B. asper	110							1	7	15	26	32	17	10	1	1			18	81	10	1			
B. asper (variant)	142		3	14	32	36	19	14	16	6	1	1					1	68	73						
*O. quathlambae**	34																						12	18	4
B. calidus	283			2	12	64	101	79	18	5	2						16	206	61						
B. erubescens	110			1	22	30	39	11	4	2	1						1	91	18						
		28	29	30	31	32	33	34	35	36	37	38	39	40											
**O. quathlambae*	34	1			2	2	4	6	1	8	4	2	1	2											

TABLE 4.

Distribution frequency of lateral line scales in *Barbus afer*, *B. afer* (Gamtoos), *Barbus asper*, *B. asper* (variant).

		Lateral line scales																				
Population	N	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
B. afer																						
Sundays	40					3	4	4	12	8	9											
Swartkops	30						3	4	10	2	5	4	1	1								
Baakens	5						1	2			1	1										
Kromme	30	1	2	3	4	9	6	1	2	1	1											
B. afer (Gamtoos)																						
Couga	30										1	7	13	9								
Wit	10											1	4	5								
Loerie	10										1	3	5	1								
B. asper (variant)																						
Bloukrans	30							2	2	6	7	8	4	1								
Groot (Natures Valley)	30					1	1	1	7	5	8	5	2									
Keurbooms	22									3	6	10	3									
Knysna	30					1		3	3	7	9	4	3									
Goukamma	30									6	4	11	8		1							
B. asper																						
Groot (Gamtoos)	30												5	10	6	5	3	1				
Meiringspoort	30												1	3	7	6	5	4	2	1	1	
Van Wyksdorp	20													1	4	3	5	5			1	1
Kammanassie	30											1	4	12	7	3	2	1				

variation (from 25 to 45 lateral line scales) is twice that of any other species (or most African cyprinids). Furthermore no single redfin population including the very small scaled *O. quathlambae* approaches this range of variation. Acceptance of this option is against taxonomic consistency and is therefore rejected. The second option (Fig. 18B) in which three taxa are recognised including typical *B. afer*, typical *B. asper* and an intermediate form (*B. afer* (Gamtoos) and *B. asper* (variant) combined) is also rejected because the degree of range overlap between the groupings is too large for practical taxonomic purposes. In addition this option is not supported by other characters. The third option (Fig. 18C) where two taxa are recognised *viz.*, *B. asper* and a taxon that combines *B. afer*, *B. afer* (Gamtoos) and *B. asper* (variant), is the most acceptable, when all aspects are taken into consideration. This choice is the solution adopted in this revision. There is a minimum of overlap in counts between the two groupings presented and the range of variation within the groups is consistent with the range of lateral line scales of other redfin species. The fourth alternative (Fig. 18D), selecting two broadly overlapping taxa *viz.*, *B. afer* and a taxon combining *B. asper*, *B. asper* (variant) and *B. afer* (Gamtoos), is less optimal and not as strongly supported by other characters such as pigmentation and length of the gut.

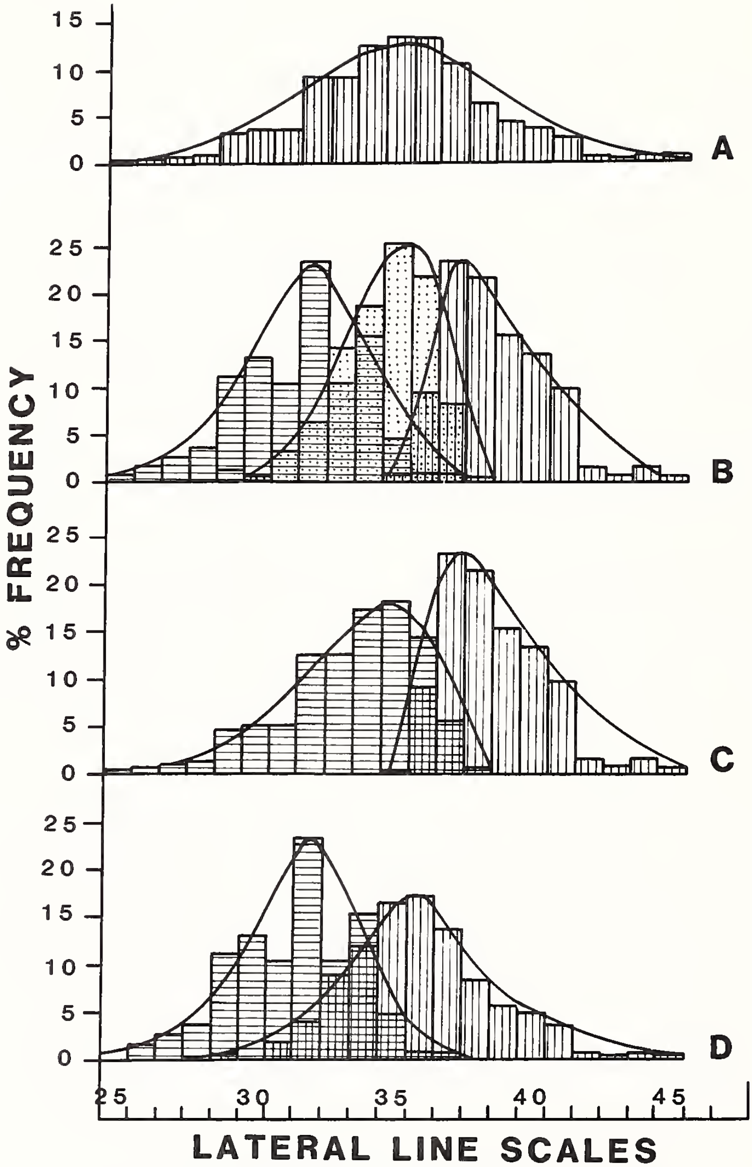

Fig. 18. Frequency distribution (%) of lateral line scales of *B. afer* and *B. asper*. A. All samples of both species combined. B. *B. afer*, *B. afer* (Gamtoos) + *B. asper* (variant), and *B. asper*. C. *B. afer* + *B. afer* (Gamtoos) + *B. asper* (variant), and *B. asper*. D. *B. afer*, *B. asper* + *B. afer* (Gamtoos) + *B. asper* (variant). Graph curves added by eye to assist interpretation.

Squamation.

Barnard (1943) referred to a crowding of the nape scales in *B. asper* and *B. tenuis*. In *B. tenuis* the nape appears to be naked in some specimens. Scales over the breast region (from the isthmus to between the pectoral fins) of the flexible rayed species are small and embedded. In the small-scaled species *B. asper* and *O. quathlambae* the "naked" area extends beyond the pectorals to the belly region. The breast scales are not markedly reduced in *B. calidus* and *B. erubescens*.

Many cyprinid fishes have an elongated or triangular scale in the axil of the pelvic fins and this is true of the great majority of southern African species. A small axillary scale of this nature is present in *B. calidus* and *B. erubescens* but not in the other redfin species. In *O. quathlambae* the basal region of the pelvic, dorsal and anal fins is fleshy and without scales (and in life is bright red in colour—Skelton, 1974a).

Scale radii

Reports that the number of scale radii increase with age in cyprinids (Chu, 1935, Barnard, 1943, Jenkins and Lachner, 1971) suggest that the character should be used with caution in the taxonomy of these fishes. The number of scale radii of the juveniles and adults of four redfin species is given in Table 5. There is very little indication that the number of radii increases with age in these species. Discrepancies in the number of radii counted here and reported on for the same species by Barnard (1943) are probably due to the differences in interpretation of what constitutes primary radii.

The number of scale radii of the redfin species is given in Fig. 19 . Examples of the scales of the redfin species are illustrated in Fig. 20. The scales of *B. tenuis* are distinctive for having a relatively large number of primary and secondary radii, whereas *B. burchelli* and *B. burgi* have relatively few radii. The difference in the number of primary radii for *B. calidus* and *B. erubescens* is diagnostic (Skelton, 1974b). Another apparent difference that has not been quantified is the position of the scale focus. In *B. calidus* and *B. erubescens* the focus is closer to the anterior margin of the scale but it is more-or-less centrally located in the flexible-rayed species.

Vertebrae

The distribution frequency of various vertebral counts of redfin species is given in Table 6. Most species have modal counts of 36 or 37 vertebrae except *O. quathlambae* which has 39 and *B. calidus* and *B. erubescens* which have 37–38. The higher number of vertebrae in *O. quathlambae* is due to a greater number of precaudal vertebrae (Table 6B) whereas the increase in *B. calidus* and*B. erubescens* appears to be due to a slight increase in the number of caudal vertebrae.

Intraspecific variation in vertebral number is spread over three to five units. The number of vertebrae before the dorsal fin often correlates with the predorsal distance. *B. burgi* for example has fewer predorsal vertebrae than other redfins and is also the species with the shortest predorsal distance (see above). The dorsal fin of *B. calidus* is relatively far back, originating well behind the origin of the pelvic fins. The species also has a relatively high mode of predorsal vertebrae.

The pre-anal vertebral count is not often given in the literature. Interspecific overlap in this count is broad so it is interesting to record an exceptional case in intraspecific variation: the modal count of most populations of *B. burchelli* is 19 or 20, however, in a sample of nine

TABLE 5.

A comparison of primary scale radii from specimens of different sizes in four redfin species.

Species	N	SL (range) (mm)	$\overline{M}$ radii/scale
B. burchelli	13	31–39	9
	17	40–68	9,7
B. phlegethon	29	27,5–39	11,9
	30	43–57	12,2
B. tenuis	10	30–39	14,1
	18	41,5–66	16,5
B. erubescens	7	30,5–35,6	13,1
	30	62–95	13,6

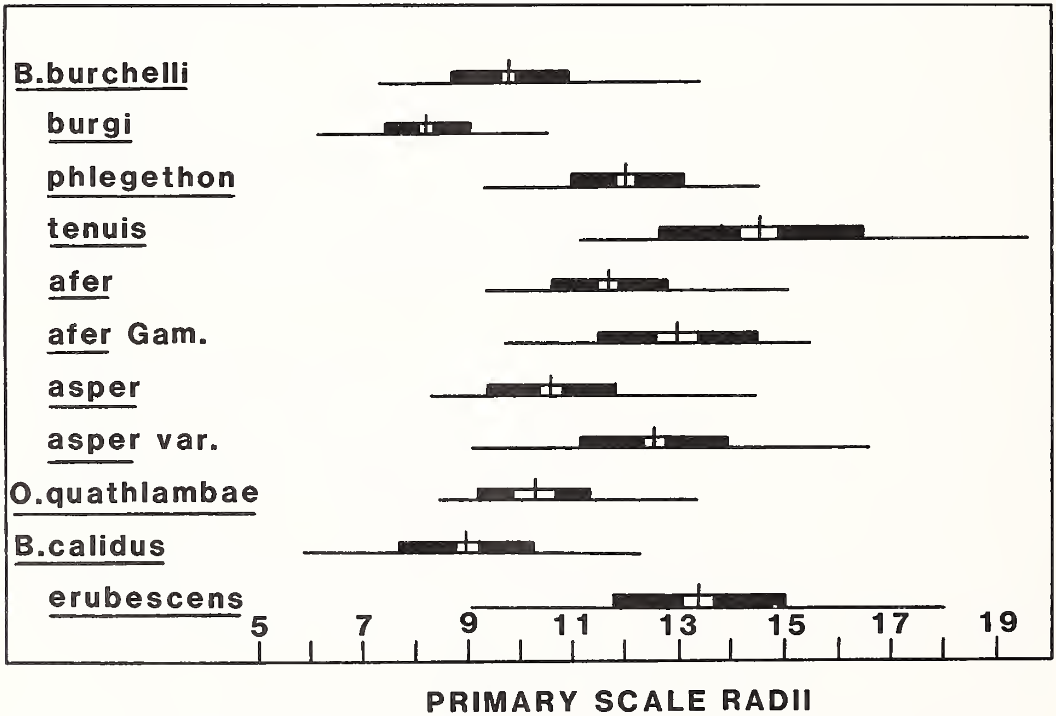

Fig. 19. The number of primary scale radii of redfin minnows.

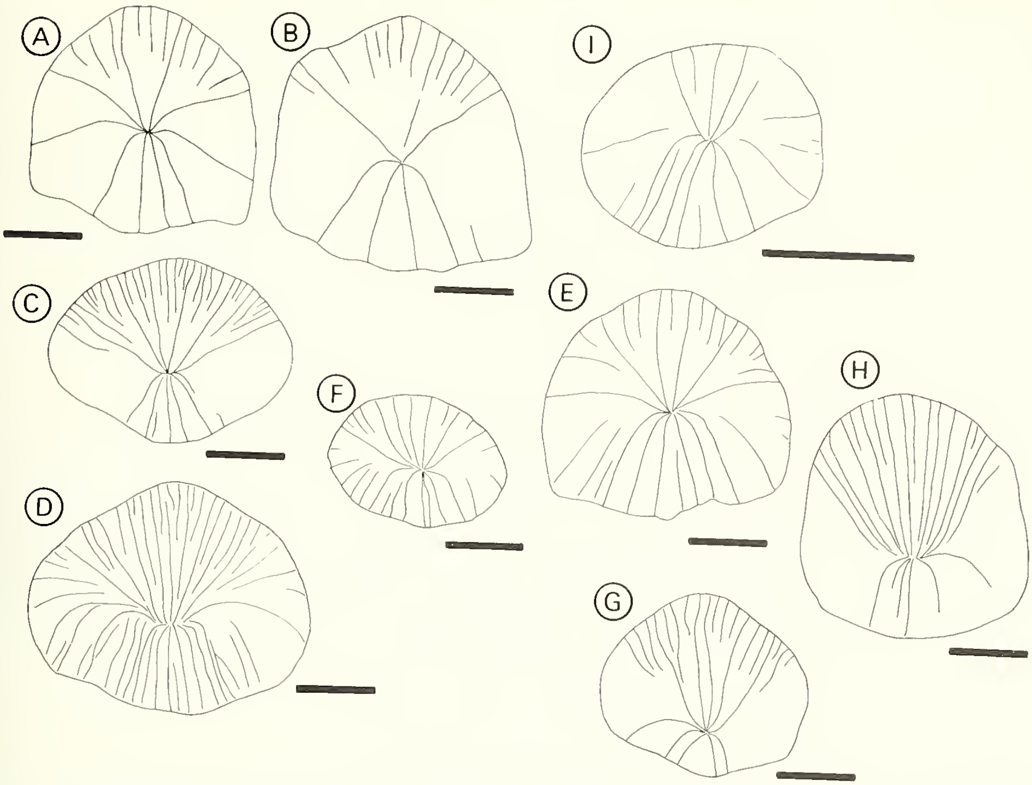

Fig. 20. Representative scales of redfin minnow species. Scale bar = 1mm. A. *B. burchelli*, B. *B. burgi*, C. *B. phlegethon*, D. *B. tenuis*, E. *B. afer*, F. *B. asper*, G. *B. calidus*, H. *B. erubescens*, I. *O. quathlambae*.

specimens from the Wit River (Bain's Kloof) seven specimens have 21 and two have 22 pre-anal fin vertebrae. This population stands out in other respects (pharyngeal teeth, mouth form and gut length) and its taxonomy warrants further attention.

Supraneural bones

Supraneural bones are well developed only in the serrated-rayed redfin species. *B. erubescens* has modal counts of six or seven supraneurals and *B. calidus* seven or eight (Table 7).

Pharyngeal bones and teeth

Three aspects of the pharyngeal bones and teeth were considered *viz.*, the length to width ratio of the pharyngeal bones, the number of teeth on the bones (tooth formula) and the form and shape of the teeth.

The length to width ratio of the pharyngeal bones of redfin species is shown in Fig. 21. The flexible-rayed species all have a similar lower ratio than the serrated-rayed species, i.e. the flexible-rayed species have relatively broader bones than the two serrated-rayed species.

Table 6.

Distribution frequency of vertebral counts in redfin species

Species	N	A. *Total vertebrae*								B. *Precaudal vertebrae*					
		33	34	35	36	37	38	39	40	17	18	19	20	21	22
B. burchelli	167		1	15	85	59	7			3	60	76	28		
B. burgi	135			6	53	67	8	1		2	36	75	23		
B. phlegethon	146			25	111	10				6	95	45			
B. tenuis	104	1	2	16	46	37	2			14	59	31			
B. afer	95			1	12	63	18	1			22	61	12		
B. afer (Gamtoos)	50				26	24					10	34	6		
B. asper	114			7	68	36	3			2	36	69	7		
B. asper (variant)	138			6	81	46	5			5	56	69	8		
O. quathlambae	31						3	16	12			1	9	16	5
B. calidus	369				27	227	111	4		1	95	265	8		
B. erubescens	151				1	80	67	3			25	122	4		

Species	N	C. *Caudal vertebrae*						D. *Predorsal vertebrae*							E. *Preanal vertebrae*				
		15	16	17	18	19	20	10	11	12	13	14	15	17	18	19	20	21	22
B. burchelli	167	3	19	50	73	20	2		61	103	3				2	82	67	14	2
B. burgi	136		8	46	60	20	2	7	82	45						29	88	19	
B. phlegethon	146		1	56	85	4			1	83	60	2			1	30	104	11	
B. tenuis	104		3	23	50	28			12	64	28			1	12	69	22		
B. afer	95		1	11	55	28			11	75	9					24	66	5	
B. afer (Gamtoos)	50		3	19	25	3				40	10					14	35	1	
B. asper	114		2	48	58	6			15	89	10				5	62	43	4	
B. asper (variant)	138		8	46	54	25	4		10	113	15				1	98	35	4	
O. quathlambae	31			2	10	14	5				6	22	3				1	24	6
B. calidus	369			12	181	160	15			70	263	36					52	268	49
B. erubescens	151			1	64	80	6		3	123	25						10	129	112

Chu (1935) showed that there is a general correlation between the feeding habits and length-width ratio of the pharyngeal bones of Chinese cyprinids; the more slender the bones the greater the tendency towards a carnivorous diet. The fact that *B. calidus* and *B. erubescens* have more slender bones than the flexible-rayed species does support Chu's (1935) findings because there are several other characters such as mouth form, gut length and pharyngeal tooth shape which suggest that the two former species are more carnivorous than most of the latter group of species. Within the flexible-rayed species as a group there are considerable differences in the teeth, tooth formula and gut length and the similarity of the length-width ratio of their pharyngeal bones is remarkable in the face of this diversity.

The distribution frequency of pharyngeal teeth of the redfins is given in Table 8, and a summary of the modal tooth counts is provided in Table 9. The usual *Barbus* formula of

TABLE 7.

Distribution frequency of supraneural bones in *B. calidus* and *B. erubescens*.

		Supraneurals				
Species	N	5	6	7	8	9
B. calidus	258	4	35	137	78	4
B. erubescens	134	—	50	81	3	—

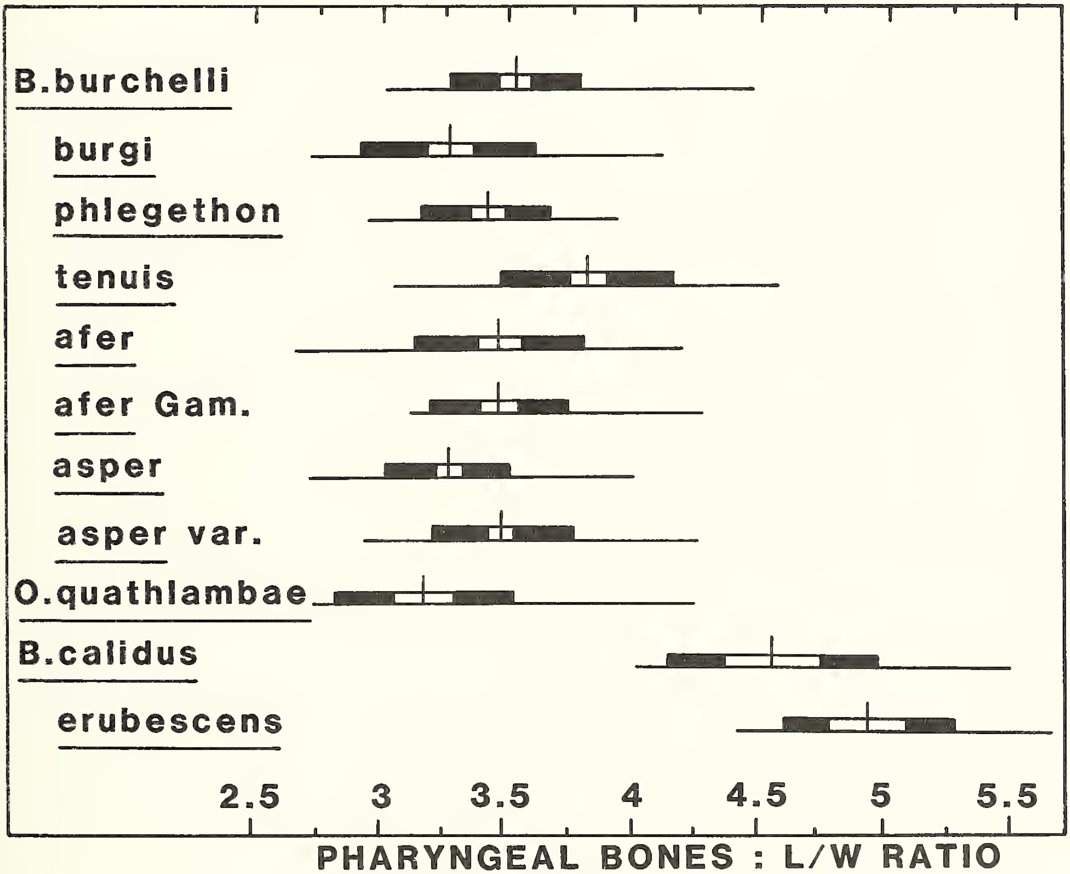

Fig. 21. The length/width ratio of the pharyngeal bones of redfin minnows.

Table 8.

Distribution frequency of pharyngeal teeth of redfin minnows.

		Left pharyngeal											*Right pharyngeal*									
		Outer row teeth			Middle row teeth				Inner row teeth				Inner row teeth				Middle row teeth				Outer row teeth		
Species	N	0	1	2	1	2	3	4	2	3	4	5	2	3	4	5	1	2	3	4	0	1	2
B. burchelli	61		10	51		9	52			1	15	45		2	15	44		7	54			10	51
B. burgi	30		10	20		4	26			1	9	20		1	6	22		6	22			9	19
B. phlegethon	32	5	24	3	1	5	26			4	13	15		1	8	23	1	6	25		6	24	2
B. tenuis	34	33	1			6	28			1	8	25		1	7	26	1	7	26		33	1	
B. afer	39	1	15	23		1	38			2	7	30		1	10	29		6	34		4	12	24
B. afer (Gamtoos)	30	2	13	15	1	2	27			1	9	20			8	22		5	25		2	12	16
B. asper	40	2	4	34		3	37			4	6	30		4	11	25		2	38			5	35
B. asper (variant)	50	5	14	31		8	41	1		4	18	28		1	14	35		4	46			16	34
O. quathlambae	12	11	1		1	4	7				12			1	11				12		12	1	
B. calidus	58		6	52		4	53	1		3	14	41		2	22	35		9	49	1		5	54
B. erubescens	30		4	26		2	28		1	6	23			6	24			3	27			3	27

Table 9.

Modal number of pharyngeal teeth in redfin species

	Left pharyngeal teeth			Right pharyngeal teeth		
Species	Row: O	M	I	Row: I	M	O
B. burchelli	2	3	5	5	3	2
B. burgi	2	3	5	5	3	2
B. phlegethon	1	3	5	5	3	1
B. tenuis		3	5	5	3	
B. afer	2(1)*	3	5	5	3	2(1)*
B. afer (Gamtoos)	2(1)*	3	5	5	3	2(1)*
B. asper	2	3	5	5	3	2
B. asper (variant)	2(1)*	3	5	5	3	2(1)*
O. quathlambae		3	4	4	3	
B. calidus	2	3	5	5	3	2
B. erubescens	2	3	4	4	3	2

O—outer (minor) row
M—middle row
I—inner (major) row
*certain populations

2, 3, 5–5, 3, 2 (Chu, 1935, Matthes, 1963, and Banister, 1973) is characteristic of most redfin species but tooth loss does occur in several of the species: *B. erubescens* has only 4 inner or major row teeth; *B. phlegethon* usually has only a single outer or minor row tooth; and *O. quathlambae* and *B. tenuis* have lost the minor tooth row entirely. There is also a tendency toward tooth loss from the outer row in some populations of *B. afer* and *B. asper* (variant).

An increase in the number of pharyngeal teeth was rarely encountered (Table 8). Of the seven specimens found with additional teeth, five are *B. burchelli* and four of these are from the same sample (collected in the Wit River, Bain's Kloof). Specimens from this sample also have the longest gut length for the species, display exceptional range of lip development and have more pre-anal fin vertebrae than other specimens of *B. burchelli*. One specimen each of *B. tenuis* and *O. quathlambae* was found with an outer row tooth. In the case of *O. quathlambae*, the specimen is the only one available from the Moremoholo River that was examined for this character and the possibility of others from this locality having minor row teeth cannot be ruled out.

The pharyngeal teeth of the redfins have not been previously described apart from those of *O. quathlambae* (Greenwood and Jubb, 1967). The shape of the pharyngeal teeth of the flexible-rayed redfin species conforms to a basic pattern which differs from that of the two serrated-rayed species. This pattern is evident in all the species despite the fact that there is considerable modification of shape in accordance with varied food habits.The evidence suggests that there has been convergence in the shape of the teeth for some of the species.

Scanning electron micrographs of the pharyngeal teeth are shown in Figs 22, 23 and 24. The crowns (occluding surfaces) of the three larger major row teeth of *B. burchelli*, *B. burgi*, *B. phlegethon* (Fig. 22a, b, and c respectively), *B. afer* and *B. asper* (Fig. 23a–d) are broad, recurved and obliquely spatulate in form. Each tooth has a major conical cusp as well as a smaller secondary cusp on the outer margin of the occlusion surface. The stems of these upper teeth in the row tend to be depressed and ovoid in cross-section. The fourth tooth in the row is stout and has a large major cusp and either one or two smaller secondary cusps of which the outer is usually the larger. The fifth tooth in this outer row is usually small and peg-like. The teeth on the inner rows are smaller but generally similar in shape to the major row teeth.

The pharyngeal teeth of *B. tenuis* (Fig. 22d) and *O. quathlambae* (Fig. 24e and f) are similar with the crowns only slightly expanded or spatulate and the major cusp recurved and placed obliquely on the outer rim of the crown. A secondary cusp is present at the outer base of the major cusp. There is also an inner secondary cusp on the fourth tooth in the row. The stems of the teeth are cylindrical and rounded in cross-section.

Of the flexible-rayed redfins the pharyngeal teeth of *B. tenuis* and *O. quathlambae* are most similar to the two serrated-rayed species *B. calidus* (Fig. 24a and b) and *B. erubescens* (Fig. 25c and d). The pattern of the teeth of the latter two species is nevertheless distinct from the pattern of all flexible-rayed species. The teeth of *B. calidus* have cylindrical stems and a narrow recurved crown with a prominent terminal hooked cusp. There are ridge rims on either side of the crown and no distinct secondary cusps. The teeth of the two inner rows are smaller versions of the upper major row teeth. The major row teeth of *B. erubescens* are stout and peg-like with a large pointed terminal cusp. Only the uppermost tooth is recurved to any extent.

The major differences between the shape of the pharyngeal teeth of the two redfin groups are that the flexible-rayed species have spatulate crowns with the major cusp off-set to the outer rim and a secondary cusp on this outer rim, whereas the serrated-rayed redfins have cylindrical

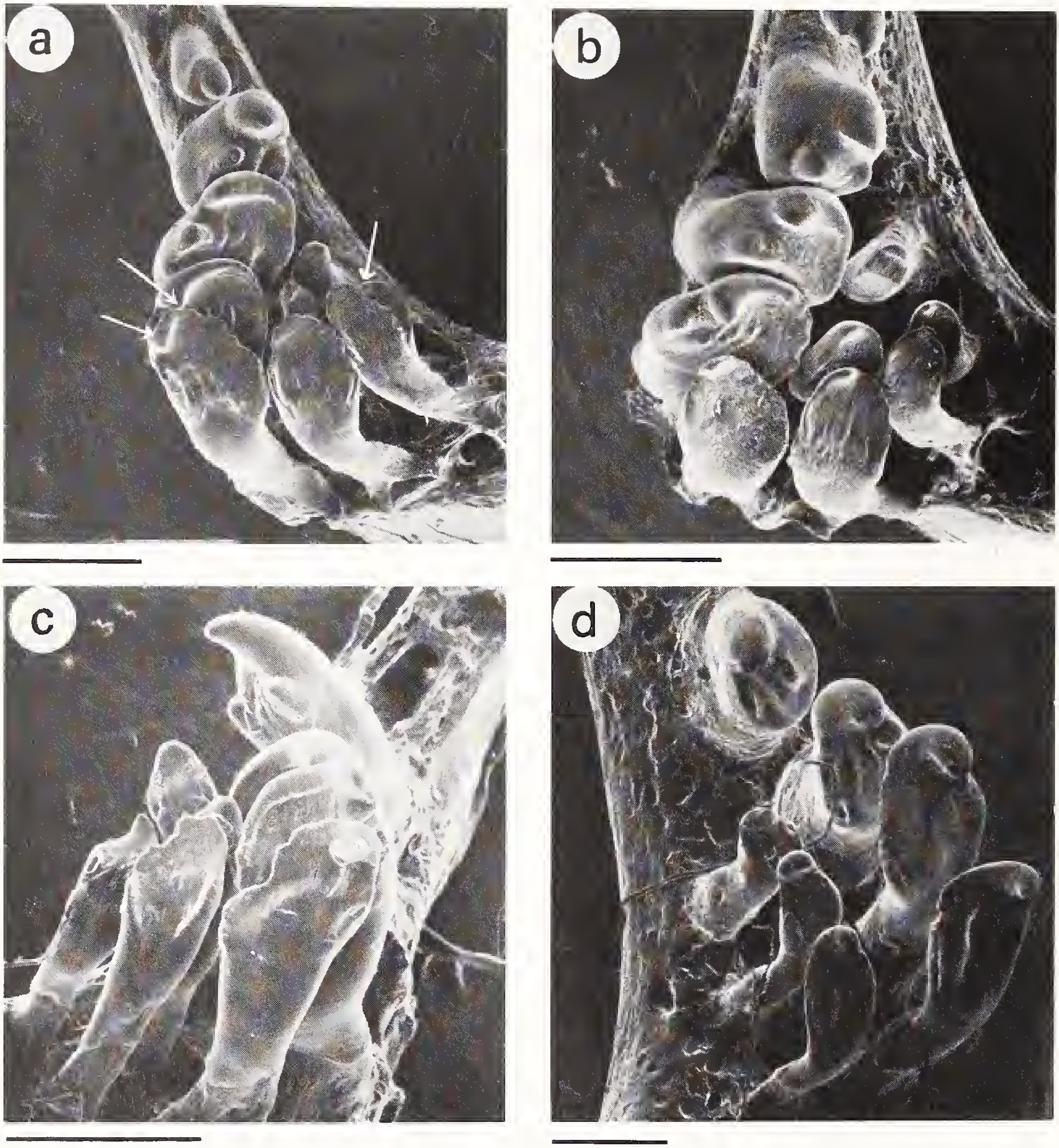

Fig. 22. The occlusal view of the pharyngeal teeth of redfin minnows. Scale bar = 0,5 mm. a. *B. burchelli*, AMG/P 1566, 52,5 mm SL, right arch; arrows direct to the lateral placement of major cusps. b. *B. burgi*, AMG/P 1847, 41 mm SL, right arch. c. *B. phlegethon*, AMG/P 722, 46 mm SL, left arch. d. *B. tenuis*, AMG/P 1935, 66 mm SL, left arch.

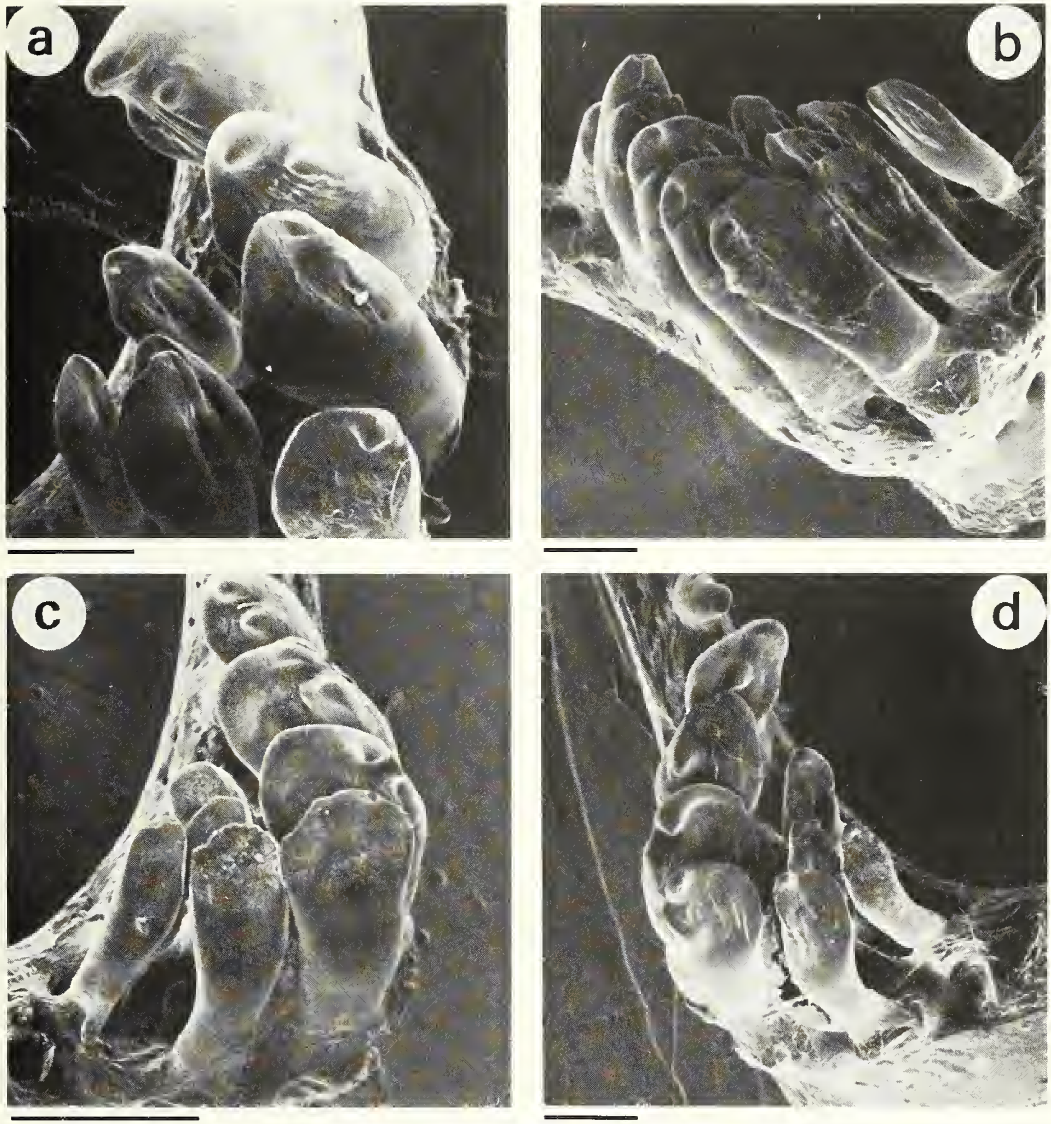

Fig. 23. The occlusal view of the pharyngeal teeth of redfin minnows. Scale bar = 0, 5 mm. a. *B. afer*, AMG/P 3460, 53 mm SL, left arch. b. *B. afer* (Gamtoos), AMG/P 1415, 58 mm SL, right arch. c. *B. asper*, AMG/P 1744, 47 mm SL, left arch. d. *B. asper* (variant), AMG/P 2656, 56 mm SL, right arch.

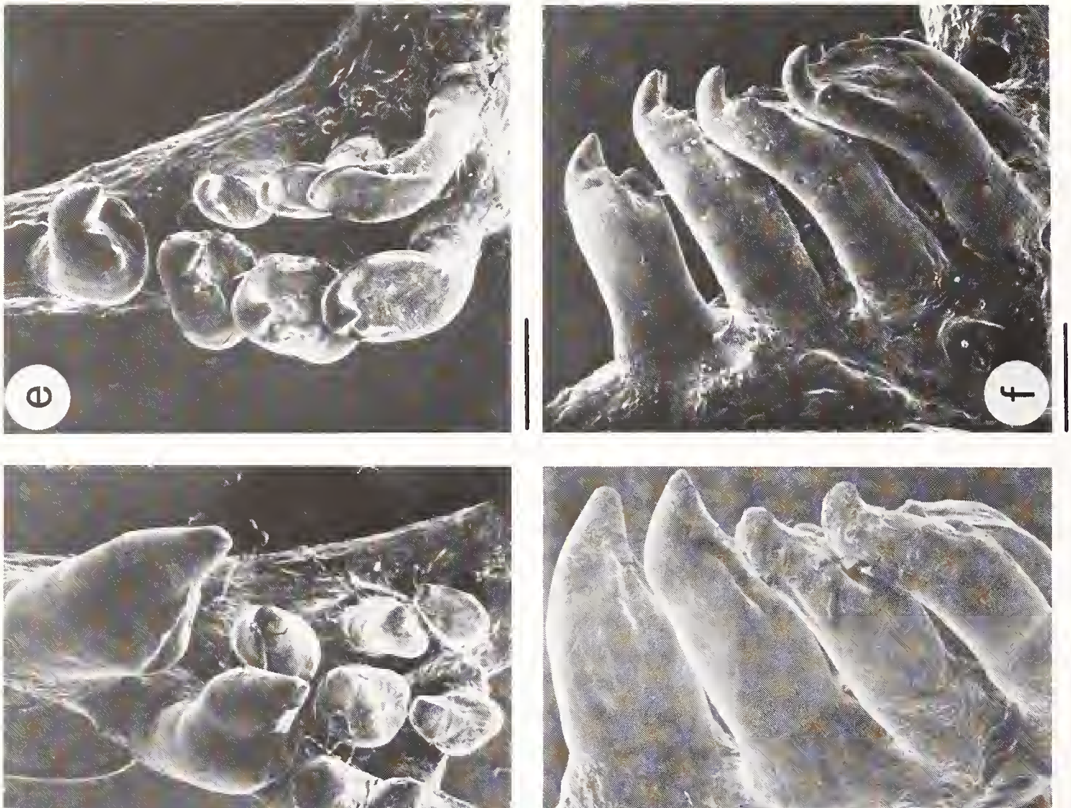

Fig. 24. Occlusal and lateral (postero-medial) views of the pharyngeal teeth of redfin minnows. Scale bar = 0,5 mm. a and b. *B. calidus*, AMG/P 1844, 65 mm SL, right arch. c and d. *B. erubescens*, AMG/P 1866, 65 mm SL, right arch. e and f. *O. quathlambae*, AMG/P 1877, 82 mm SL, right arch.

teeth with narrow crowns and large conical or pointed terminal major cusps and no distinct secondary cusps.

Gut length and coiling pattern

In fishes as well as in other animals the length of the gut (or alimentary canal within the body cavity) is most often correlated with the diet of the species (Nikolsky, 1963, Weatherley, 1972, and Ribble and Smith, 1983). Short guts are associated with carnivory and increasing gut length is associated with an increasing tendency to herbivory. Gut length and pattern of coiling or flexure have been used as a systematic character in fishes in general (e.g. Kafuku, 1958, and Yamaoka, 1985), frequently so in cyprinids. For most smaller African cyprinid species gut characteristics have not been described or well used as a taxonomic character. On the whole very little attention has been paid to the gut of redfin species. Smith (1841) mentioned that his sub-genus *Pseudobarbus* (which included *B. burchelli*) was characterised by the "intestinal canal long and contorted". Greenwood and Jubb (1967) referred to the short gut of *O. quathlambae*, which character was one of the reasons why the species was removed from the genus *Labeo*.

Redfin species show a relatively wide range of gut length (Fig. 25). Three characteristic groups of regression lines are formed by the plots of gut length against standard length for the various species or, in two cases, for different populations of a species. Short guts that more or less equal the standard length characterize four species, *B. tenuis*, *B. calidus*, *B. erubescens* and *O. quathlambae*. Gut lengths of about 2–2,5 times the standard length in adults characterize a second group which includes *B. burchelli*, *B. burgi* (in part, specimens from the Berg River system except those from the locality Groot Drakenstein), *B. phlegethon*, *B. afer*, *B. afer* (Gamtoos), and *B. asper* (variant). Relatively long guts which in adults exceed 2,5 times the standard length characterizes the third group which includes *B. asper*, and the Verlorevlei and Groot Drakenstein populations of *B. burgi*.

The pattern of involution or coiling of the gut of the redfins is illustrated diagrammatically in Fig. 26. The increase in length for the different species is accommodated by progressive involution within the same pattern. The species with short guts usually only have a single "S" flexure which may become slightly more involuted in *B. tenuis*. The intraspecific variation of gut length increases markedly with increasing gut length.

Mouth

B. calidus and *B. erubescens* have large terminal "U"-shaped mouths and all other redfins have sub-terminal or inferior crescent-or sickle-shaped mouths, with relatively thick lips. An exceptional degree of intraspecific variation in mouth form is found in the population of *B. burchelli* from the Wit River in Bain's Kloof in which the usual lips (Fig. 27A) are retracted from the lower jaw and replaced by a firm but not keratinised sheath (Fig. 27B).

Tubercles

Head, body and fin tubercles are prominent features of many cyprinid fishes (Wiley and Collette, 1970, and Collette, 1977). For African cyprinids tubercles are better known in the bariliine and labeine species than they are for the barbines (e.g. Howes, 1980, and Reid, 1985). The large tubercles of certain redfins are well known (Barnard, 1943, and Jubb, 1965 and 1967). Recently Cambray and Stuart (1985) gave some details of the development of tubercles in *B. burchelli*. In the present study the tubercles and the pattern they form is described for all the redfin species as these structures have been found to be useful as taxonomic characters.

Two kinds of tubercles are present in the redfins: *B. calidus* and *B. erubescens* have minute

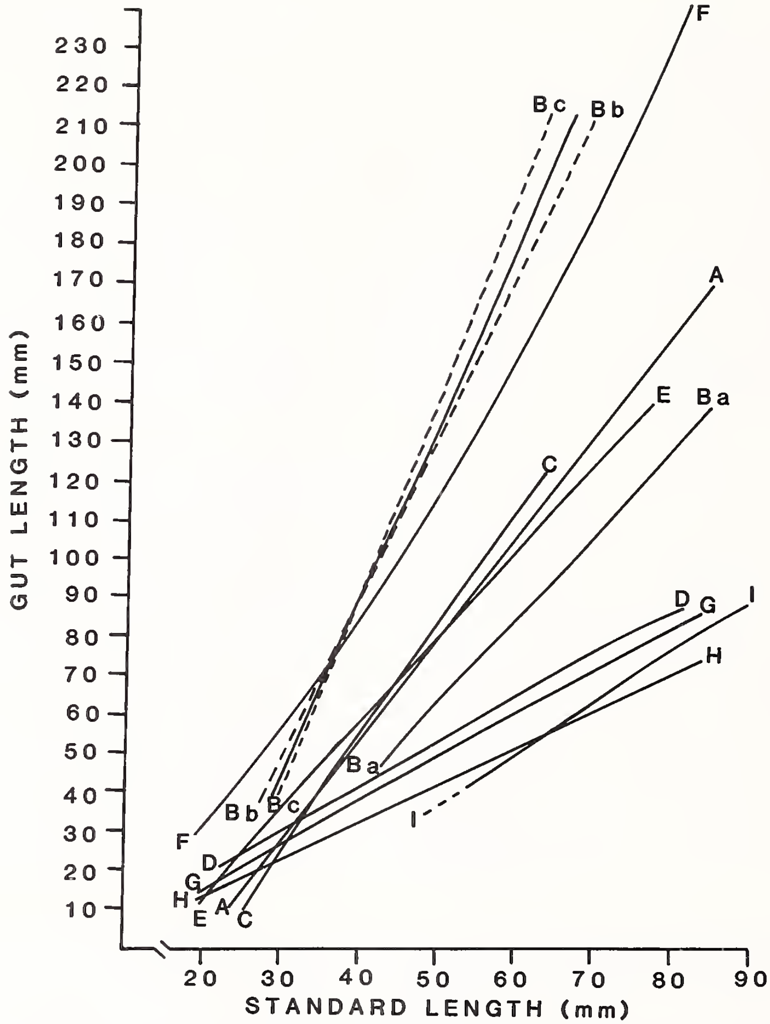

Fig. 25. The length of the gut of redfin minnows as given by lines of regression. A. *B. burchelli*, Y= −50,5 + 2,6X, r^2 = 0,8651. B. *B. burgi*, (a) Y = −51,2 + 2,26X, r^2 = 0,8414, (b) Y = −81 + 4,3X, r^2 = 0,9051, (c) Y = −119 + 5,25X, r^2 = 0,9263. C. *B. phlegethon*, Y = −63,75 + 2,9X, r^2 = 0,8564. D. *B. tenuis*, Y = −4,4 + 1,1X, r^2 = 0,9026. E. *B. afer*, Y = −31,83 + 2,24X, r^2 = 0,9495. F. *B. asper*, Y = 0,36 × $X^{1,47}$, r^2 = 0,8901. G. *B. calidus*, Y = −8,5 + 1, 13X, r^2 = 0,9528. H. *B. erubescens*, Y = −5,58 + 0,93X, r^2 = 0,9656. I. *O. quathlambae*, Y = −30,8 + 1,34X, r^2 = 0,8995.

"erupted pimples", and the flexible-rayed species have small and large conical tubercles. Conical tubercles are deciduous, hypertrophied epidermal structures with a distinct outer layer or cap of keratin (Fig. 28c). These develop on the head, scales and fins of adult males, especially during the spring and summer months (Barnard, 1943, and Cambray and Stuart, 1985). Tubercle buds and small tubercles also occur on larger females (pers. obs., and Cambray and Stuart, 1985). The

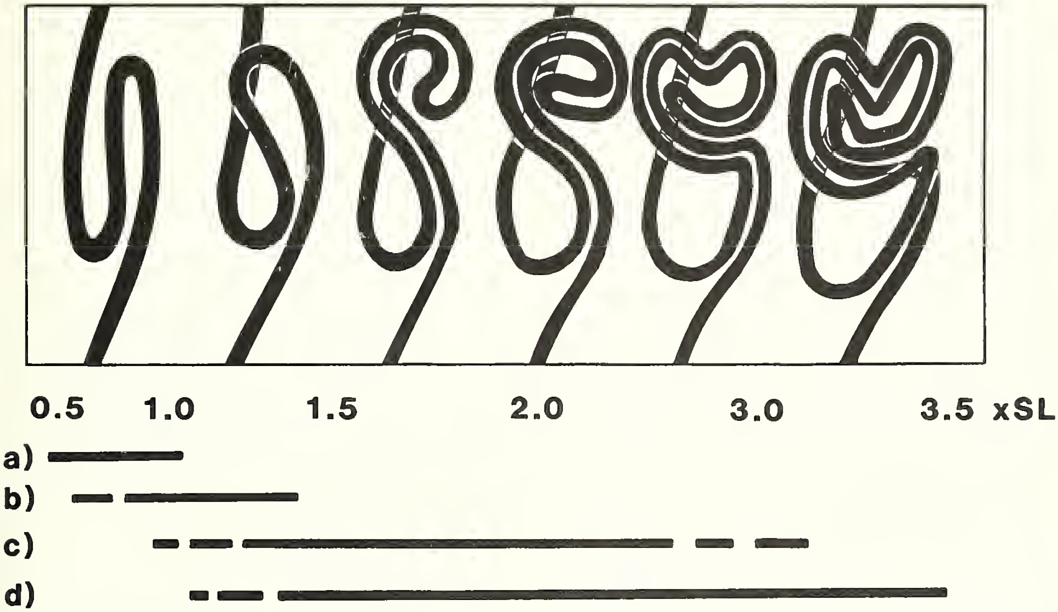

Fig. 26. Coiling pattern of the gut in redfin minnows, giving indication of correlation of length with standard length (SL) and the range of length variation and extent of involution for each species. a. range of *B. calidus*, *B. erubescens* and *O. quathlambae*. b. range of *B. tenuis*. c. range of *B. afer*, *B. burchelli*, and *B. phlegethon*. d. range of *B. asper* and *B. burgi*.

fact that the tubercles are correlated with sexual maturity and breeding condition strongly suggests that they have some function associated with breeding activity. In *B. burchelli* the first signs of wear and sloughing off of the larger tubercles was in November when spawning commenced. Cambray and Stuart (1985) suggest that this indicates they are used to defend a territory. The smaller tubercles on the scales and fins of the flexible-rayed species (see Figs 28, 29 and 30) are, however, more likely to be involved in a body contact function, probably during the spawning act itself (Wiley and Collette, 1970, and Collette, 1970).

There are differences in the size and degree of development of tubercles among the flexible-rayed redfins but a common pattern of distribution seems to exist within the group. For comparative purposes this pattern will be described for *B. burchelli* (Fig. 31). The actual number of tubercles on the head of an individual depends on several factors including age (size), and time of the year. Younger smaller fishes have fewer tubercles than older larger specimens. A peak of development occurs during the summer months around November–January. The pattern of tubercle distribution on the head of *B. burchelli* is as follows: bilateral groups of tubercles develop on the snout. The median tubercles here can measure up to 1,8 mm basal diameter and 1,6 mm in height, and there are five or six tubercles in each group. A row of progressively smaller tubercles extends in an arc above each nare to the antero-dorsal edge of the orbit and then continues posteriorly along the dorsal edge of each orbit. A number of generally smaller tubercles are scattered irregularly over the crown of the head. Apart from the occasional one, tubercles are not found on the cheeks, below the orbit or on the ventral surface of the head.

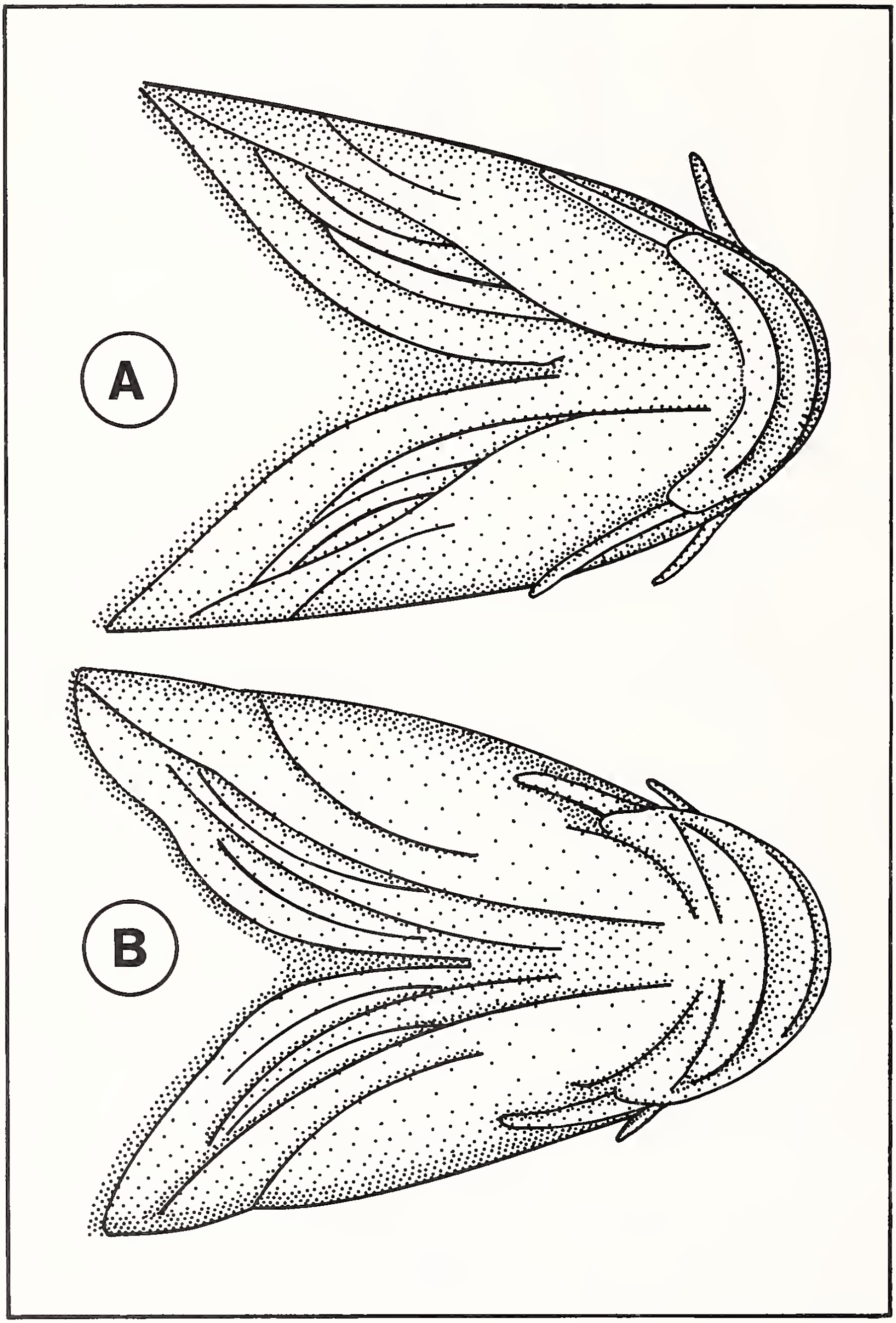

Fig. 27. Examples of different mouth forms in *B. burchelli* : A. lower lips not retracted, specimen from AMG/P 4972, and B. lips retracted from rim of lower mandible, specimen from AMG/P 1411.

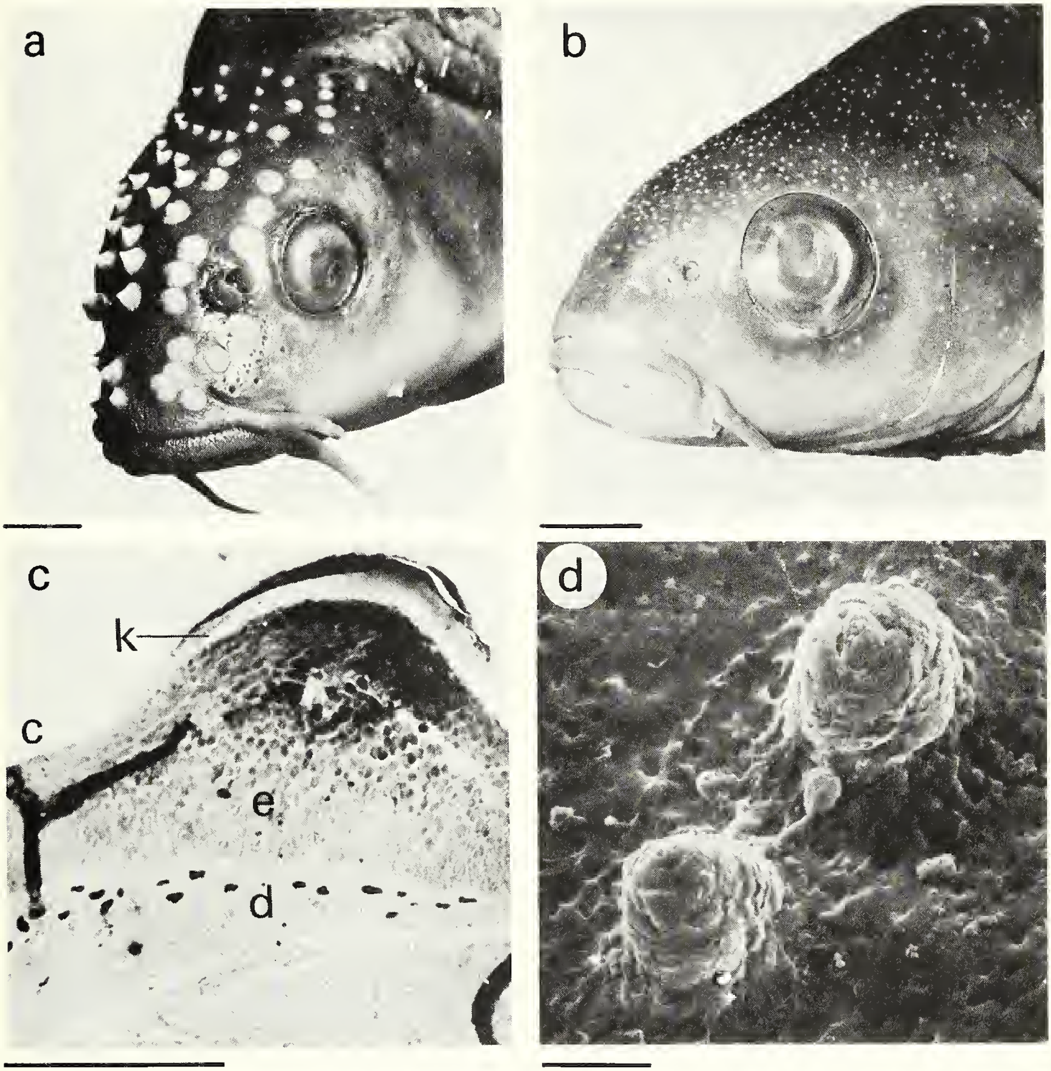

Fig. 28. Aspects of head tubercles of redfin minnows. a. *B. burchelli*, AMG/P 7223, 99 mm SL. Scale bar = 5 mm. b. *B. erubescens* (paratype), AMG/P 2074, 85 mm SL. Scale bar = 5 mm. c. Section of head tubercle from *B. afer* AMG/P 3786. c—canal, d—dermis, e—epidermis, and k—keratin. Scale bar = 0,3 mm. d. *B. erubescens* (paratype), AMG/P 2074, head tubercles, SEM. Scale bar = 0,05 mm.

From five to ten small (about 0,08 mm diameter) conical tubercles are arranged in a single linear series along the free edge of most of the scales of sexually mature males (Fig. 29c). Chest and belly scales only lack these tubercles. Bands up to five or six across (about 0,6–0,7mm in width) develop on the dorsal side of the pectoral fin branched rays (Fig. 29a). The individual

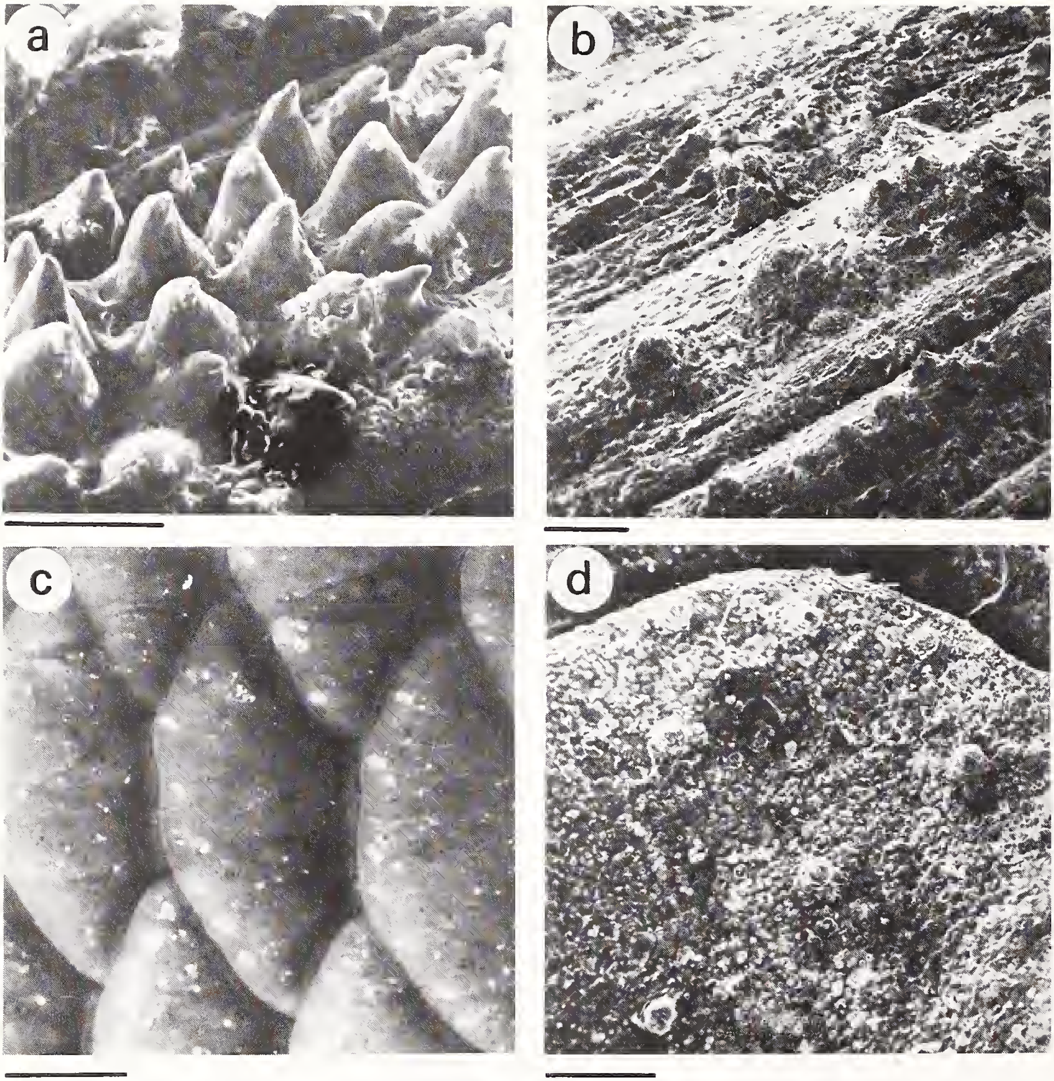

Fig. 29. Tubercles on the pectoral fins and scales of redfin minnows. a. *B. burchelli*, AMG/P 2077, pectoral fin tubercles. Scale bar = 0,1 mm. b. *B. erubescens*, AMG/P 2074, pectoral fin tubercles. Scale bar = 0,25 mm. c. *B. burchelli*, AMG/P 3472, body scales. Scale bar = 1,0 mm. d. *B. erubescens*, AMG/P 2074, scale. Scale bar = 0,25 mm.

tubercles in the bands are small, from 0,1–0,2 mm diameter. Single rows of tubercles develop on the fin rays of other fins.

The tubercles of *B. burgi* are similar to but relatively smaller than those of *B. burchelli*. Well developed tubercles on the snout of a large specimen (78 mm SL) of *B. burgi* measure 0,8 mm

diameter and height. They are also more numerous and each group on the snout has from 10 to 15 tubercles.

The tubercles of *B. phlegethon* are seldom observed probably because of all the redfin species they are the most poorly developed (Fig. 30b and d). Both Barnard (1943) and Jubb

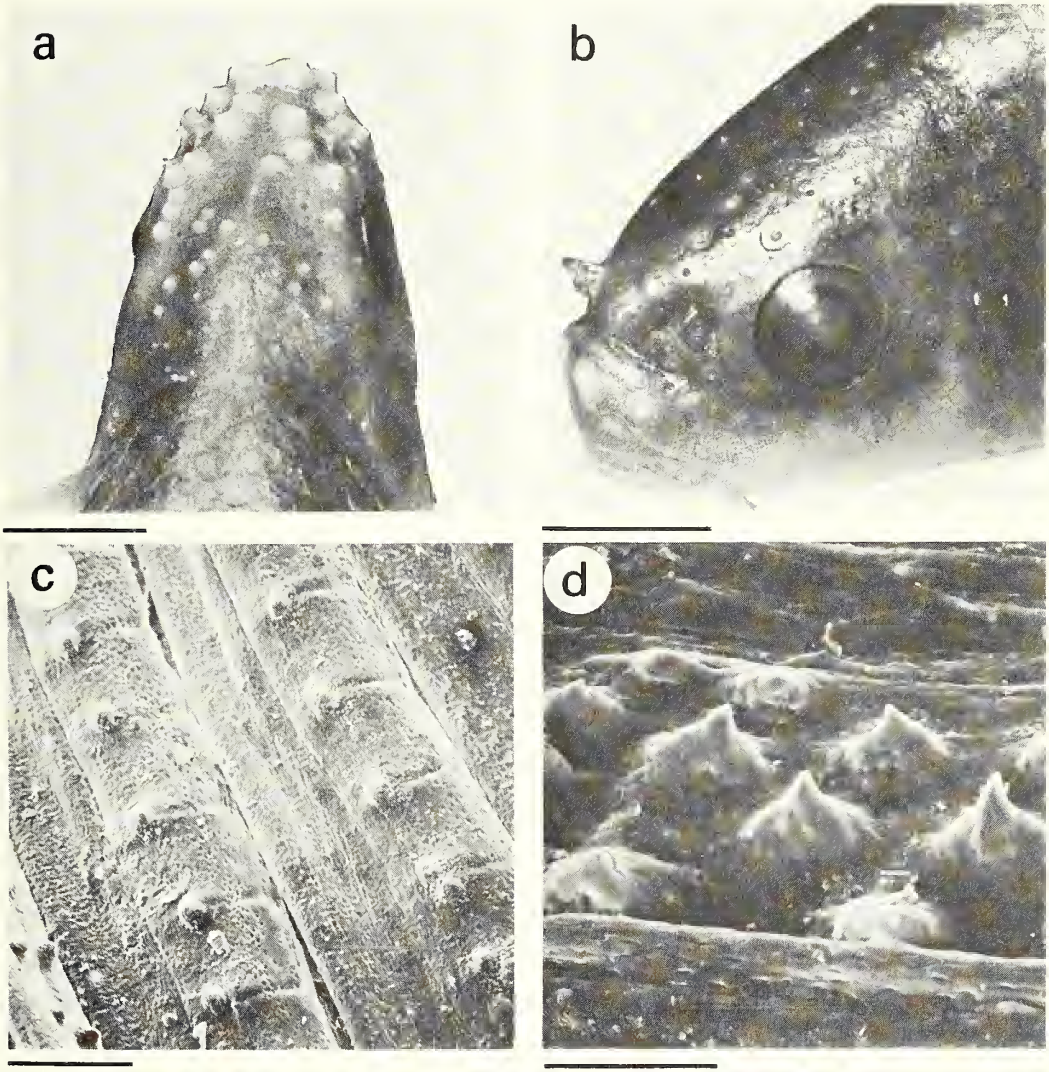

Fig. 30. Tubercles of redfin minnows. a. dorsal view of head of *B. tenuis*, AMG/P 3455, 62 mm SL. Scale bar = 5 mm. b. head of *B. phlegethon*, AMG/P 7366, 70 mm SL. Scale bar = 5 mm. c. *B. tenuis*, AMG/P 3455, pectoral fin. Scale bar = 0,25 mm. d. *B. phlegethon*, AMG/P 1399, pectoral fin. Scale bar = 0,1 mm.

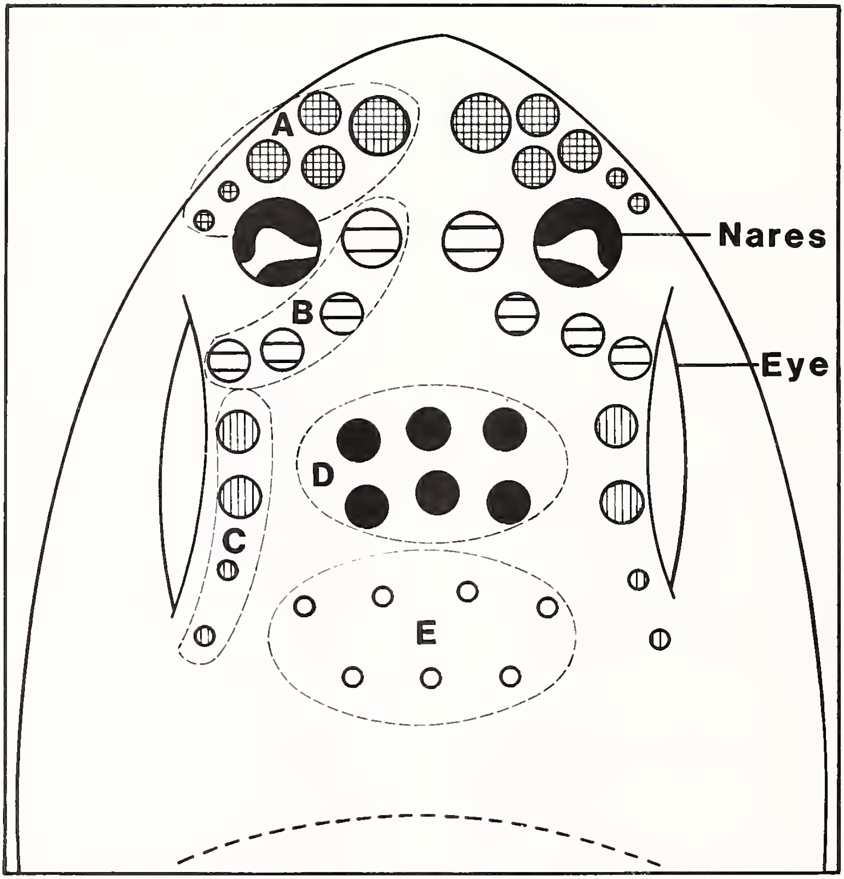

Fig. 31. Diagrammatic representation of pattern of head tubercles on flexible-rayed redfin minnows. A. cluster on snout, B. row above nares, C. row above orbit, D. anterior dorsal cluster, E. posterior dorsal cluster.

(1965 and 1967) did not report tubercles on this species. The tubercles occur in the same pattern on the head as for *B. burchelli* and weak bands are found on the pectoral fin rays but tubercles have not been observed on the scales of *B. phlegethon*.

Contrary to the findings of Barnard (1943) and Jubb (1965 and 1967) tubercles have also been observed on *B. tenuis* (Fig. 30a and c). Again the head pattern is similar to *B. burchelli* but there are fewer tubercles on the snout (four or five per group). Tubercles in single widely-spaced rows only occur over the pectoral fin rays (Fig. 30c) and rays of other fins. In this species a linear row of tubercles occurs along the free edge of each body scale (apart from those on the ventral surface).

Large conical head tubercles are characteristic of the males of both *B. afer* and *B. asper*. Jubb (1965 and 1967) has a photograph of the heads of two tubercled males of *B. asper* (variant) from the Homtini River. There are from three to five tubercles per group on the snout and the

tubercles on the top of the head tend to be clustered into an anterior and a posterior group. The scales have a single marginal row and there are bands of tubercles (two to three across) over the pectoral fin rays.

Skelton (1974a) described and illustrated the tubercles of *O. quathlambae*. In this species the head tubercles are more numerous and smaller than in any other flexible-rayed redfin but they are distinctly conical and the basic pattern is the same. By way of exception tubercles do occur over the operculum and below the orbit. Each scale has one or two tubercles only and there are well developed bands of compressed tubercles on the pectoral fin-rays. Single tubercle rows occur on other fins.

There are no large conical tubercles on the head of *B. calidus* or *B. erubescens*. Breeding adults of both sexes of these two species develop tiny (0,1 mm diameter) epidermal excrescences (Fig. 28b and d) called "pimples" by Barnard (1943). The pimples are scattered over the head dorsum as well as in clusters over the opercula and cheeks. Similar pimples are scattered over the exposed surfaces of the scales (Fig. 28d). Single widely-spaced rows occur on the rays of all fins (Fig. 29b). The tubercles are usually better developed in males than in females.

Live colour and pigmentation

Live specimens of all the redfin species were observed during the course of the study. Different ecological and physiological situations clearly affect the expression of colour and pigmentation of individuals but descriptions characteristic of each species are still useful for taxonomic purposes. Colour illustrations of redfin species have been given previously by Smith (1841), Jubb (1965 and 1967), Smith and Smith (1966) and Skelton (1974a).

For all species the predominant background colours are olivaceous browns and greens which may vary from a light yellowish gold to deep olive or even steel-blue (as recorded by Skelton (1974a) for *O. quathlambae*). Ventral parts are usually lighter, either white or pale cream. The opercula are metallic silvery-gold with a red infusion as a result of the superficial presence of bloodvessels. The iris of the eye is golden and the pupil black. The fins are distinctive with the proximal portions becoming orange in juveniles and intensifying to bright scarlet in adults, especially males during the breeding season (spring and summer). The caudal fin is least affected by this red colouration but it can be fairly intensely coloured in certain individuals. The red colour impinges onto the adjacent body region in *O. quathlambae* to a greater extent than in the other species. The males of *B. erubescens* in breeding dress become suffused with red. The red colour of the fins persists in adults through the winter although to some extent the intensity fades at this time.

Certain markings on the body are broadly characteristic of the various species. These are represented diagrammatically in Fig. 32. *B. burchelli* juveniles, sub-adults and younger adults have irregular dark blotches on the dorso-lateral surface including a linear mid-lateral series which ends in the form of a large triangular mark at the base of the caudal fin. In older adults the pattern is obscured by a deepening of the general pigmentation. *B. burgi* is similar to *B. burchelli* although there is more frequently a tendency to form a single lateral band or connected series of blotches. In some populations (e.g. that of Verlorevlei) a series of thin wavy horizontal bands passes along the body below and more particularly above the lateral band.

Adult *B. phlegethon* are probably the most striking redfins having black blotches over the dorso-lateral surface and being silvery-white ventrally. The juveniles of this species have a prominent thin lateral stripe and lack the dark patches of the adults. *B. tenuis* is plain with a dark

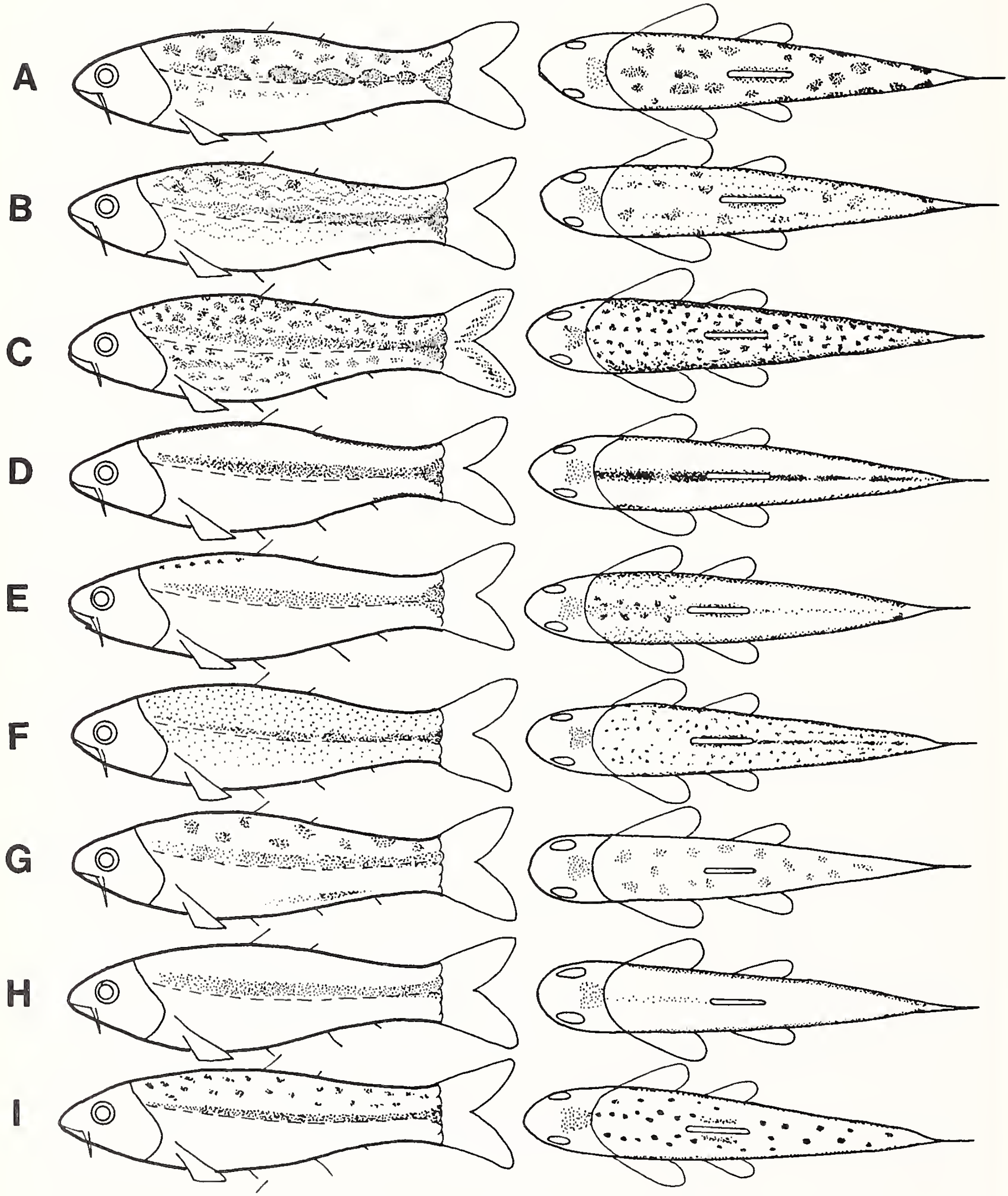

Fig. 32. Diagrammatic representation of pigmentation of redfin minnows. A. *B.2burchelli*, B. *B. burgi*, C. *B. phlegethon*, D. *B. tenuis*, E. *B. afer*, F. *B. asper*, G. *B. calidus*, H. *B. erubescens*, I. *O. quathlambae*.

mid-lateral band from behind the head to the base of the caudal fin, and a dark mid-dorsal stripe which is sometimes interrupted to form a series of dashes.

The individuals from most populations of *B. afer* have a mid-lateral body stripe that tends to expand at the base of the caudal fin and a bi-lateral series of predorsal spots. A mid-predorsal stripe is present in some populations. The dark waters of the Tsitsikama coastal rivers where *B. asper* (variant) occurs cause this species to be very dark itself but careful examination often shows the underlying pattern to be similar to that of *B. afer*. *B. asper* was described by Barnard (1943) as being like a "speckled hen" which is a result of the scale centres being darkly pigmented. There is often also an uneven or interrupted lateral stripe from the head to the base of the caudal fin in this species.

O. quathlambae usually has a dark lateral band and a bi-lateral series of discrete predorsal spots, dashes or vermiculations (Skelton, 1974a, and Gephard, 1978: Fig. 2).

The pigment patterns of *B. calidus* and *B. erubescens* are sufficiently distinct to be used to differentiate the two species (Skelton, 1974b). *B. calidus* has a broad broken lateral band and large irregular dark patches along the dorsal side. There is also a dark stripe along the base of the anal fin and usually a midventral stripe on the caudal peduncle. By way of contrast *B. erubescens* has only an unbroken lateral band from behind the head to the base of the caudal fin and a light mid-predorsal stripe.

Cephalic lateral line canals

The pattern of cephalic lateral line canals has not been used previously as a taxonomic character for southern African *Barbus* species. Although the overall pattern is similar for all the redfins there are differences in the degree of development between the two "serrated-rayed" and the "flexible-rayed" species (Fig. 33). In the former the canal system is continuous and a short median branch passes postero-dorsally from the supra-orbital canal. This branch is not present on the flexible-rayed redfins in addition to which the preopercular-mandibular canal is separate from the post-ocular commissure and the mandibular canal is reduced or absent. The mandibular canal is only developed as a short tube on the postero-lateral part of the dentary in *B. burchelli* and*B. burgi*. In *B. burgi* the connecting tube on the angulo-articular bone is frequently absent.

Osteological characters

A full description of the osteology of the redfin and other southern African *Barbus* species is being presented elsewhere (Skelton, in prep. b). The main differences are between the flexible- and the serrated-rayed groups which are considered to represent different phylogenetic lineages. A summary of the main points of comparison between the two groups is given in Table 10. Specific differences within these groups are summarised in Table 11 for the serrated-rayed species and Table 12 for the flexible-rayed species.

TAXONOMIC CONCLUSIONS

The outstanding problems in redfin taxonomy since Jubb (1967) concern the identity and limits of two pairs of closely similar species, *B. burchelli*–*B. burgi* and *B. afer*–*B. asper*. The recognition of each of these species depends on the taxonomic interpretation of certain morphological characteristics. A further problem concerns the taxonomic status of the group as a whole. Are the redfins monophyletic, and, if so, what is their generic status, or, if not, then what is the generic status of the different lineages? The phylogeny of the redfins will be

TABLE 10.

A comparative summary of aspects of osteology of redfin species.

	B. burchelli	*B. burgi*	*B. phlegethon*	*B. tenuis*
Neurocranium shape	moderately deep subrectangular	deep subrectangular	deep, narrow subrectangular	shallow, broad subrectangular
Supraethmoid	shallow groove	shallow groove	shallow groove	unossified, shallow groove
Lateral ethmoid, entopterygoidcondyles	concave	concave	concave	concave
Pterosphenoids	divided	divided	divided	divided
Supraorbitals	stout	stout	stout	reduced–irregular
Supraorbital shelf	wide notched	wide notched	wide notched	narrow–notched(?)
Infraorbitals				
(a) lachrymal	low peak	low peak	low peak	low peak
(b) dermosphenotic	triangular	broad-square	triangular	reduced-triangular
Exoccipitals	flanged	flanged	flanged	slender process
Intercalars	vestigial. irreg.	vestical. irreg.	vestical. irreg.	vestical. irreg.
Extrascapulars	irregular	irregular	irregular	irregular
Basioccipital process	flat; 30–40°	flat; 30–40°	flat; 30–40°	flat; 30–40°
Opercle	moderate	moderate	moderate	broad
Preopercular canal	complete	complete	reduced	reduced
Hyomandibular		narrow, tall	short, broad	
Metapterygoid (dorsal edge)	convex	convex	convex	convex, deep notched
Quadrate	shallow excav.	shallow escav.	shallow escav.	shallow escav.
Premaxilla	deep	deep	deep	deep
Maxilla	deep	deep	deep	deep
Lower jaw	short flange	short flange		
Urohyal	deep, tapered	deep, tapered	deep, tapered	slender, tapered
Pharyngeals	broad	broad	broad	broad
Pectoral girdle male vs female	dimorphic	dimorphic	dimorphic	dimorphic
Pelvic girdle				
Weberian neural crest	simple, irreg.	simple, irreg.	simple, irreg.	simple, irreg.
Supraneurals	absent (vestig.)	absent (vestig.)	absent (vestig.)	absent (vestig.)
Intramuscular bones	reduced	reduced	reduced	reduced
Dorsal fin (unbranched ray, pterygiophores)	slender (8)	slender (8)	slender (8)	slender (8)
Anal fin (pterygiophores)	6	6	6	6

TABLE 10.

A comparative summary of aspects of osteology of redfin species.

B. afer	*B. asper*	*B. calidus*	*B. erubescens*	*O. quathlambae*
moderate	moderate	moderate	moderate	moderate
subrectangular	subrectangular	subtriangular	subtriangular	subtriangular
shallow groove	shallow groove	deep groove	deep groove	unossified, shallow groove
concave	concave	condyles, not concave	condyles, not concave	concave
divided	divided	joined	joined	divided
stout (when present)	stout (when present)	slender	slender	vestigal irregular
wide notched	wide notched	narrow	narrow	wide notched
low peak	low peak	high peak	high peak	low peak
triangular	triangular	triangular variable	triangular variable?	
flanged	flanged	no process	no process	slender process
vest.(irreg.)	vestig(irreg.)	disc. well dev.	disc. well dev.	vestig (irreg.)
irregular	irregular	regular (?)	regular (?)	irregular
flat; 30–40°	flat; 30–40°	concave 50–60°	flat 30–40°	
moderate	moderate	suprapreopercular	suprapreopercular	broad
reduced	reduced	complete	complete	reduced short, broad
convex	convex	concave	concave	convex deep notched
shallow escav.	shallow escav.	deep excav.	deep excav.	shallow excav.
deep	deep	slender	slender	deep
deep	deep	slender long flange	slender long flange	deep
deep, tapered	deep, tapered	slender truncate	slender truncate	deep tapered
broad	broad	slender	slender	broad
dimorphic	dimorphic	monomorphic process short	monomorphic process long	dimorphic
simple.irreg.	simple.irreg.	flanged	flanged	simple irreg.
absent(vestig.)	absent(vestig.)	large	large	absent (vestig.)
reduced	reduced	well developed	well developed	reduced
slender (8)	slender (8)	stout serrated (8)	moderate (9)	slender (8)
6	6	7	8	6

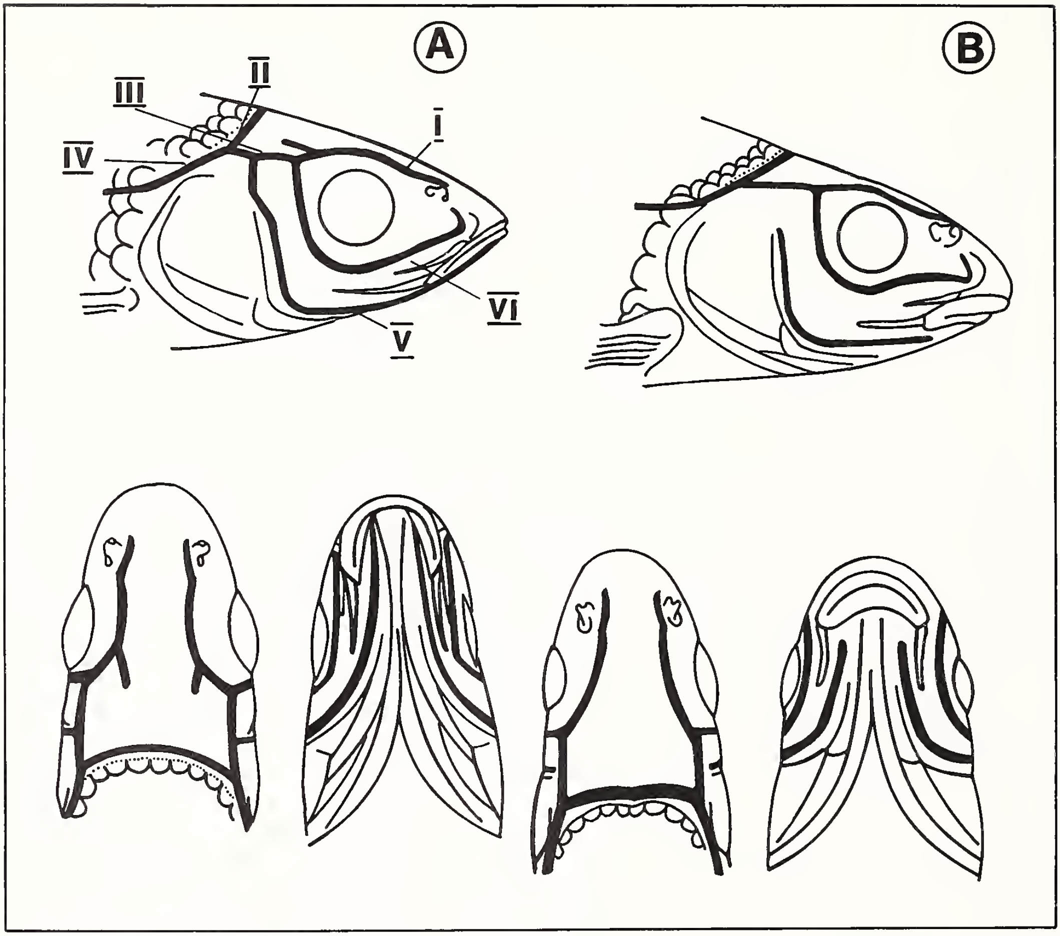

Fig. 33. Diagrammatic representation of the cephalic lateral line system of A. serrated-rayed redfins and B. flexible-rayed redfins. Canal nomenclature after Reno (1969): I. supraorbital canal, II. supratemporal canal, III. postocular commissure, IV. cephalic lateralis. V. preoperculo-mandibular canal.

addressed fully in a separate paper (Skelton, in prep. a). The specific and generic taxonomic status of the redfins is considered here in order to make the formal decisions necessary for the overall study. Before dealing with the specific taxonomic problems concerning the two species pairs mentioned above some comments on the taxonomy of the other redfin species are necessary.

As far as possible the material studied was drawn from across the geographic distribution range of each species. In the case of *O. quathlambae* little can be said on the geographic variation of the species. However, Gephard (1978) made a contribution in this regard showing that there

TABLE 11.

A summary of the main osteological differences between *B. calidus* and *B. erubescens*

Character	*B. calidus*	*B. erubescens*
Vomer	Extends beyond posterior region of lateral ethmoid.	Does not extend beyond posterior margin of lateral ethmoid.
Symplectic-Quadrate	Extends into relatively short groove. Symplectic shorter.	Extends into relatively long groove. Symplectic longer.
Opercle	less prominent dorsal process for dilatator operculi. Postero-lateral corner sharp.	More prominent dorsal process for dilatator operculi. Postero-lateral corner rounded.
Pelvic bone	Processes are short and broad.	Processes are more slender and elongate.

are a number of differences between specimens from the three, then known, populations of the species. The most divergent character measured by Gephard (1978) was body pigmentation (the other characters he considered were dorsal fin rays, anal fin rays, lateral line scales and anal fin pigmentation). Adopting Ginsberg's (1938) criteria, each population of *O. quathlambae* showed more than 90% divergence in pigmentation. The differences were nevertheless considered not worthy of taxonomic significance and, based on the the variation on scale counts, the populations were labelled as "varieties". These findings do suggest that each population has been relatively isolated from each other for some time.

Greenwood and Jubb (1967) described the unusual morphological characteristics of *O. quathlambae* in the African context and stated that these features indicated a refined degree of adaptation to a high mountain stream environment. Drakensberg mountain streams provide cold, clear, well-oxygenated waters, potentially fast currents, and shallow rocky substrates without extensive aquatic or marginal macrophytes. Colder temperatures are generally conducive to higher meristic characters in fishes (Barlow, 1961; Fowler, 1970) and this may have had an influence on the development of the vertebral and squamation characteristics of *O. quathlambae*. Gephard (1978) suggests that the species has crevice-spawning habits. Small scales and higher vertebral counts may therefore also be adaptations to enhance flexibility required for manoeuvering in confined spaces.

The reduction in the number of pharyngeal teeth to the extent of that found in *O. quathlambae* and *B. tenuis* is an extremely unusual development for African barbine species that suggests a strong selection pressure towards such reduction. In the general absence of interspecific piscine competition, it seems likely that this pressure has come from the available food source itself. In high altitude mountain streams phytogenous organic matter is usually limited (Allen, 1969) and the main source is autochthonous and allochthonous invertebrates. Benthic aquatic insects are the main food reported for *O. quathlambae* (Pike and Tedder, 1973, and Gephard, 1978). The sub-terminal mouth, short gut and form of the pharyngeal teeth are well suited for such food.

In spite of initial doubts on the validity of *B. tenuis* because of the *a priori* weakness or subsequent discreditation of Barnard's (1938 and 1943) diagnostic characteristics (body depth, absence of head tubercles, scale striae and squamation) the species proves to be soundly established. A slender profile and scales with more radiating striae than other redfin species are

TABLE 12.

A summary of osteological features of flexible-rayed redfin species.

Character	Description
Neurocranium shape	moderate—deep, subrectangular
Supraethmoid	poorly ossified, shallow groove
Lateral ethmoid condyles	concave
Pterosphenoids	divided
Supraorbitals	short & broad, reduced or vestigial in *B. tenuis* and *O. quathlambae*
Supraorbital shelf	broad, notched (narrow in *B. tenuis*)
Lachrymal	low dorsal peak
infraorbital 5	short, triangular (broad/squarish in *B. burgi*).
Exoccipitals	with flange, slender process in *B. tenuis* and *O. quathlambae*
Intercalars	vestigial, irregularly present
Extrascapulars	irregular
Basioccipital process	flat, 30–40 degrees
Opercle	moderately rectangular, shallow and broad in *B. tenuis* and *O. quathlambae*
Preopercular canal	complete, reduced in *B. phlegethon*, *B. tenuis* and *O. quathlambae*
Hyomandibular shape	moderate, narrow in *B. phlegethon*, short in *B. tenuis* and *O. quathlambae*
Metapterygoid (dorsal edge)	convex, notched in *B. tenuis* and *O. quathlambae*
Quadrate	shallow notch for symplectic
Premaxilla	relatively short and deep
Maxilla	relatively short and deep
Dentary	short flange for sensory canal present only in *B. burchelli* and *B. burgi*
Urohyal	relatively deep, mid-flange tapered
Pharyngeal bones	relatively broad
Pectoral girdle	sexually dimorphic
Weberian crest	simple, irregular
supraneurals	vestigial or absent
Intramuscular bones	reduced and weakly ossified
Dorsal fin ray	simple and flexible
Anal fin pterygiophores	6

reasonably consistent characteristics. The pharyngeal tooth formula is a strongly diagnostic character and the osteology of the species is also distinctive (Skelton, in prep. b). In the field *B. tenuis* may be recognised from the river bank by its characteristic mid-dorsal stripe (Skelton, pers. obs.). Collecting records and field observations indicate that *B. tenuis* favours smaller mountain tributaries rather than the lowland mainstreams of the Gourits system. Occasionally it occurs together with *B. asper* but this may be because of reduced environments from water abstraction for agricultural use.

Intraspecific variation in fin lengths and caudal peduncle proportions is recorded between

the Gourits and Keurbooms River populations of *B. tenuis*. The Keurbooms population shows longer fins and a narrower caudal peduncle.

These differences are probably induced by differences in the environments of the two systems. The Keurbooms catchment has a mean annual precipitation of 750 to 900 mm (Midgeley and Pitman,1969) whereas comparable stream catchments of the Gourits receive from 400 to 500 mm. It is likely therefore that the flow regime of the Keurbooms is greater than the Gourits tributaries and the observed morphological differences are those which are known to respond in similar fashion in other cyprinids (e.g. Hubbs, 1940, Barlow, 1961, and Stewart, 1977).

Barbus phlegethon is the smallest redfin species and is characterised by distinctive pigmentation, a relatively deep and narrow body, a small mouth with very short barbels, and weakly developed secondary male sexual characters. It is restricted in distribution to a few tributaries of the Olifants mainstream and a single isolated population in the small Driehoek stream in the Cedarberg mountains (Fig. 34). There is a degree of geographical variation between populations of tributaries of the Olifants mainstream and the Driehoek population in the number of dorsal fin branched rays. Seven branched rays is the modal number for the dorsal fin of redfin species including *B. phlegethon* but six of ten specimens from the Driehoek population have only six branched rays. The Driehoek specimens also have a higher number of pectoral fin rays (mode 15 *vs* 13–14 from mainstream populations) and more lateral line scales (36–39 usually 37 or 38 *vs* 29–37 with a mode of 35 for mainstream populations). Several specimens in the Driehoek sample are larger than normally encountered for this species and one of these is a male with the best developed tubercles yet observed for this species.

The Driehoek stream differs from the mainstream valley tributaries of the Olifants River in factors such as altitude, gradient and physical dimensions. The altitude of the Driehoek is 900–1 200 m whereas the valley tributaries where *B. phlegethon* occurs are between 200–400 m. The Driehoek is a small stream (2–3 m wide and generally less than 0,5 m deep) with a low gradient and a sandy-gravel substratum whereas the valley tributaries are larger streams (5–10 m wide and up to 1,5 m deep), characterised by rocky pools and flowing stretches with a substratum of well-worn (i.e. smooth and rounded) loose rocks and pebbles. The Driehoek population may have been relatively isolated for some time and it is therefore possible that both genotypic and phenotypic factors are responsible for the observed morphological differences.

A summary of the main differences in external morphology and skeleton between *B. calidus* and *B. erubescens* is given in Table 13. The taxonomic significance of reduced serrations of the dorsal unbranched fin ray in *B. erubescens* was discussed by Skelton (1974b). It was concluded that the development or otherwise of such serrations is not a reliable taxonomic character for *Barbus* species. The intraspecific variation in this character can be large, for example, as described by Poll (1976) for a single population of *Barbus miolepis* Boulenger. The reason or reasons for such wide variation as well as the functional significance, if any, of a serrated spiny dorsal ray in *Barbus* species is not known, although speculative suggestions are possible.

Certain functionally linked characters may show a fine degree of correlation. In *B. erubescens*, for example, the relatively minor reduction in the number of pharyngeal teeth correlates with a difference in shape of the teeth, a more slender pharyngeal bone, and shorter length of gut compared with the same of *B. calidus*. Eastman and Underhill (1973) studied intraspecific variation in the pharyngeal teeth of 42 cyprinid species and concluded that the pharyngeal bones and tooth morphology are usually consistant and therefore taxonomically

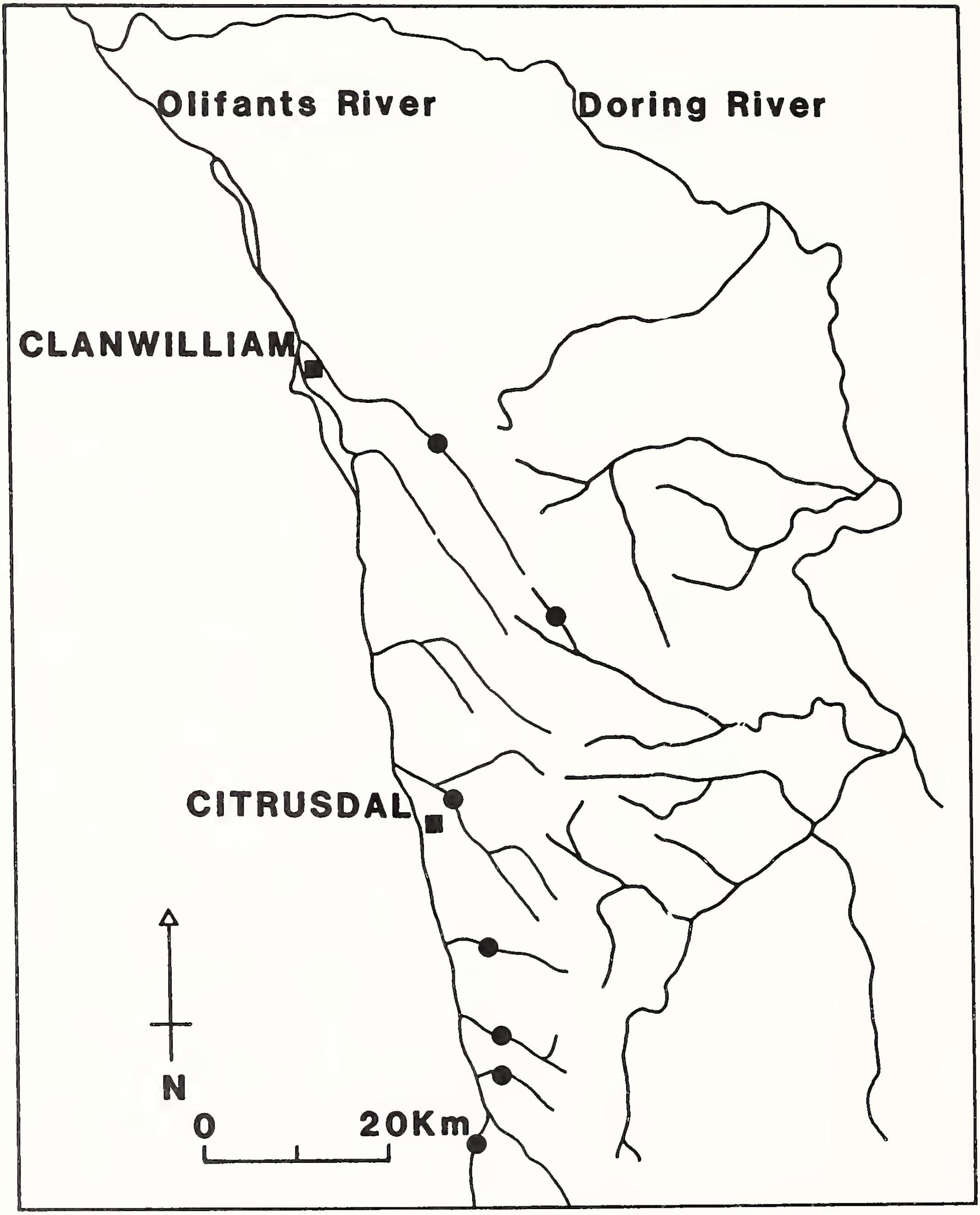

Fig. 34. Distribution of *B. phlegethon* in the Olifants River system.

TABLE 13.

A summary of certain character differences between *B. calidus* and *B. erubescens*

Character	*B. calidus*	*B. erubescens*
Orbit diameter (%HL) ($\overline{M}$)	29,1 (25–36)	26,75 (22–32)
Postorbit length (%HL) ($\overline{M}$)	43,6	46
Interorbit (%HL) ($\overline{M}$)	34,1	31,9
Caudal peduncle L.	19,5	21,1
Dorsal branched rays (mode)	7	8
Anal branched rays (mode)	6	7
Scale radii ($\overline{M}$)	9	13
Predorsal vertebrae (mode)	13	12
Pharyngeal bones L/W (+)	4,6	4,9
Pharyngeal teeth (mode)	2, 3, 5–5, 3, 2	2, 3, 4–4, 3, 2
Dorsal unbranched ray	strongly serrated	weak or no serrations
Pigmentation	broken lateral band, spotted dorsal surface	lateral stripe and plain dorsal surface
Symplectic bones	short injunction with quadrate, shallow	long injunction with quadrate, deep
Opercle	postero-ventral corner angular	postero-ventral corner rounded
Pelvic fin bones	ischial process broad, lateral prong short	ischial process slender, lateral prong long

useful for most species but tooth formulae are not always sufficiently consistent for this purpose. A similar conclusion is reached with respect to the pharyngeal teeth of the flexible-rayed redfins. For certain species, for example, *B. burgi*, *B. burchelli*, *B. asper* and *B. afer*, intraspecific variation in pharyngeal teeth and gut length is too broad to be a diagnostic taxonomic character at the species level. However, this broad variability is a character which sets these species apart from other similar-sized African barbines.

The use of barbels in cyprinid taxonomy is another feature which has stimulated much debate. Schmidt (1983) concluded that barbels are not sound generic characters and should be used with caution at the species level. The present study indicates clearly that each case should be judged on its own merits. It is necessary to examine comprehensive geographical and size-range series of a species before the taxonomic value of barbels is safely established. Barnard (1943) claimed the seemingly trivial difference in the development of the anterior barbels between *B. burchelli* and *B. burgi* indicated the real validity of the two species. This difference is consistent, however, and there are at least two other supporting characters, *viz.*, the size and shape of the last or 5th infraorbital bone and the size and number of head tubercles.

The 5th infraorbital is generally small and relatively slender in redfins and most other southern African *Barbus* species. Only in *B. burgi* does the bone develop wide flanges. Two examples of other cyprinids, in which a similar development of this bone has been used for taxonomic purposes, are given by Miller (1963) and Barbour and Miller (1978).

Head tubercles are frequently used for taxonomic purposes in cyprinid fishes. Tubercles serve a variety of functions in fishes and tubercles from different regions of the body may serve different purposes. Wiley and Collette (1970) and Collette (1977) suggested that the structures

may have evolved to assist spawning individuals to maintain contact in flowing waters. Reid (1985) indicates that the large tubercles on the head and snout of *Labeo* species may have a hydrodynamic role. There is a clear sexual or secondary sexual function for the large head tubercles of redfin species because these develop fully only on adult males during the breeding season and are worn down as the season progresses (Barnard 1943, Cambray and Stuart 1985, and Skelton, pers. obs.). Cambray and Stuart (1985) suggest that the large head tubercles are used by male *B. burchelli* in defense of territories. Territoriality of tuberculated sexually mature males of other flexible-rayed redfin species (*B. phlegethon* and *O. quathlambae*) has been witnessed in the field (pers. obs.). The difference in tubercle development between *B. burgi* and *B. burchelli* is not an easy taxonomic character to use because it has to be gauged from comparable specimens in terms of size and state of sexual maturity and activity. There may be a degree of intraspecific variation in the development of tubercles which would negate their taxonomic value (e.g. tubercles have not yet been observed on any individual specimen of *B. burgi* collected in the Verlorevlei system). In spite of such limitations a difference in size and number of head tubercles of the mature males of *B. burgi* and *B. burchelli* is recorded here and supports the taxonomic distinction between these species whose status is therefore endorsed.

Further attention should be given to the taxonomic status of the Verlorevlei population of *B. burgi*. Specimens from this site display a distinctive colour and pigment pattern (a series of thin parallel longitudinal lines and no spots), have an exceptionally long intestine and have not yet been seen with head or body tubercles.

There are few examples in the literature of a cyprinid species having as large an intraspecific variation in gut length as that found for *B. burgi*. A reversed example is provided by Lachner and Wiley (1971) for a species of chub, *Nocomis leptocephalus*. Although this species usually has a long and whorled intestine certain populations have a short "S"-flexured gut. The authors attached no special taxonomic significance to these particular populations. The broad range of and interspecific overlap of the gut length in the flexible-rayed redfin species weakens the taxonomic value of this character at the specific level. In a group context, however, the broad variation is an unusual and therefore interesting taxonomic characteristic of these species.

The question of differences in scale counts between *B. afer* and *B. asper* has been discussed already. The conclusion reached was that *B. asper* is a distinctive small-scaled species confined to the larger tributaries and mainstreams of the Gourits and Groot-Gamtoos river systems and *B. afer* is a widespread polytypic species that includes populations from the south coastal rivers referred to as *B. asper* (variant). Pigmentation and gut length characters support this arrangement although neither are independently convincing taxonomic characters. A clinal variation in several morphometric characters also supports the taxonomic fusion of "typical" *B. afer* and *B. asper* (variant) into a single polytypic species.

The presence and distribution of *B. afer* and *B. asper* in the Gamtoos River system has always been a problem on account of their close similarity. Barnard (1943) considered that only *B. asper* was present in the Gamtoos but recognised that the form found in the mountain tributaries differed from the typical form in the Groot River tributary. Jubb (1965) mentioned that specimens from certain coastal tributaries of the system were closer to *B. afer* than to *B. asper*. As there was no clear distinction between the two species, museum samples were frequently confused.

The Groot River rises well beyond the fold mountain belt in the Great Karoo. It joins the Gamtoos mainstream after abruptly turning at right angles to its course and penetrating the

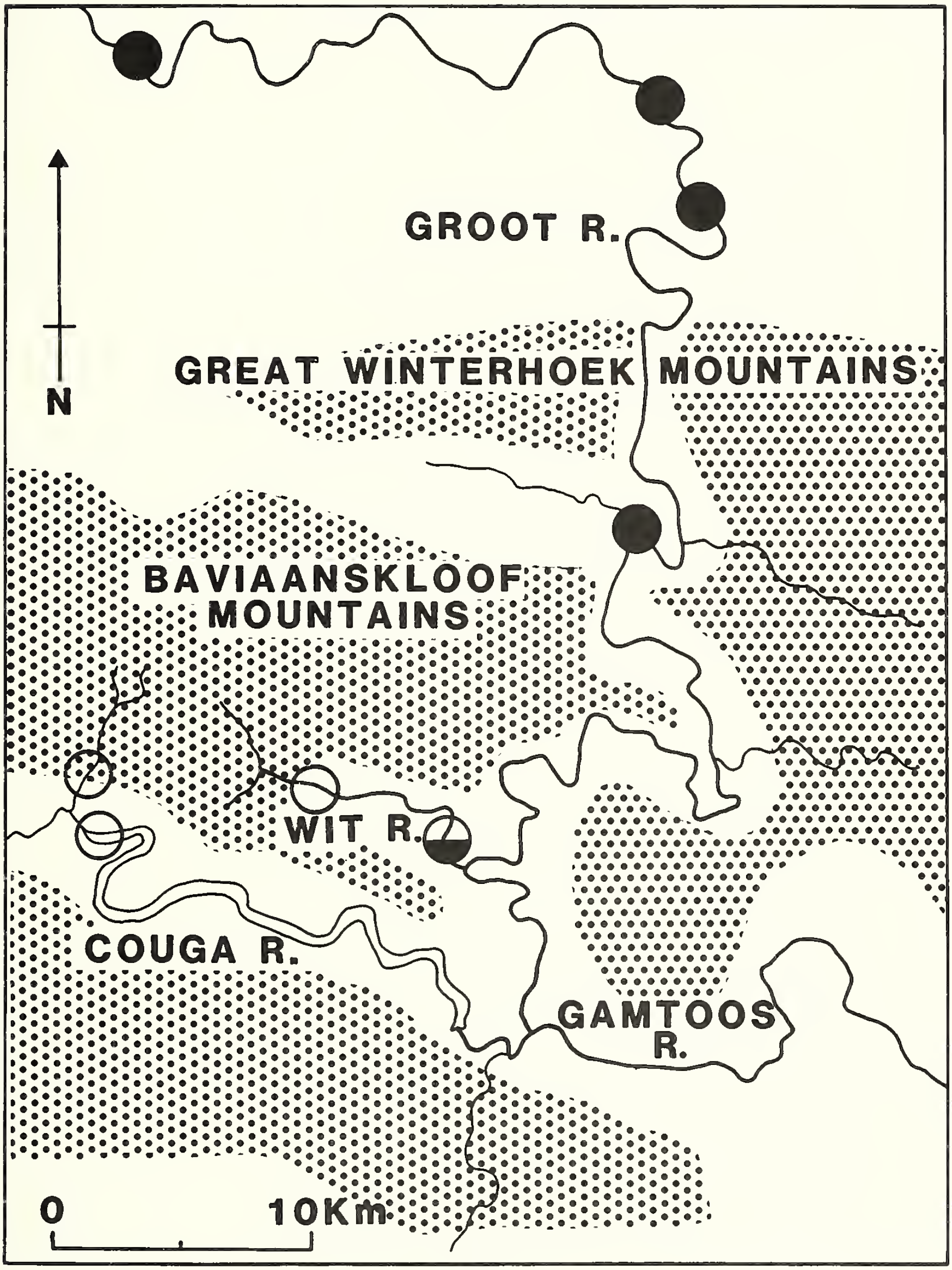

Fig. 35. Part of the Gamtoos River system showing the distribution of *B. afer* (unshaded circles) and *B. asper* (shaded circles). Site where both species collected given as half shaded circle.

Baviaanskloof-Great Winterhoek Mountains in a narrow gorge (Fig. 35). *Barbus asper* inhabits the Groot River to within the gorge whereas *B. afer* is found in the mountain tributaries of the system. Both species were collected in the lower reaches of the Wit River, a tributary that joins the Groot River within the gorge, but there is no evidence of integration of the two species at this site.

The Groot River drains Karoo sediments which impart high loads of total dissolved solids and sediments to the waters. Fold mountain tributaries are characteristically clear streams with low pH and dissolved mineral concentrations. The distribution of *B. asper* in the Groot and *B. afer* in the mountain tributaries appears to reflect distinctly different habitat preferences. This is supported by Hofmeyr's (1966) study which reported that *B. asper* was more tolerant of high chloride concentrations than *B. afer*.

The species-level taxonomic conclusions from this study may be summarised as follows: nine redfin species are recognised *viz.*, *B. burchelli* Smith 1841, *B. afer* Peters 1864, *B. asper* Boulenger 1911, *B. burgi* Boulenger 1911, *O. quathlambae* (Barnard 1938a), *B. phlegethon* Barnard 1938b, *B. tenuis* Barnard 1938b, *B. calidus* Barnard 1938b, and *B. erubescens* Skelton 1974. The interrelationships of the species will be given elsewhere (Skelton, in prep. a) but for the purpose of further discussion on their generic status it may be stated that the fairly obvious suite of differences between the two serrated-rayed species on the one hand (*B. calidus* and *B. erubescens*) and the flexible-rayed species on the other does reflect distinct phylogenetic origins of the two groups. Furthermore the phylogenetic investigation showed that, although very distinct in many ways, *O. quathlambae* is a member of the flexible-rayed monophyletic lineage. The only other formal taxonomic adjustment required is the inclusion of coastal populations of *B. asper* under *B. afer*.

GENERIC STATUS

All the redfins currently are referred to the unwieldly large genus *Barbus*. As far as reflecting phylogenetic relationships is concerned, this allocation is unrealistic and prejudicial to the classification of the species and the elucidation of their biogeography. The investigation on which the present paper is based (Skelton, 1980) also included a study of the phylogenetic relationships of the redfin species. This study showed clearly that two distinct lineages constitute the "redfins" *sensu lato*. The flexible-rayed redfin minnows form a monophyletic lineage of morphologically distinct species relative to all other *Barbus*. It is entirely in the interests of comparative biology to recognise this relationship, at least at the generic or sub-generic level. The genus traditionally embodies the concepts of relationship and distinctiveness (Bolin, 1947 and Mayr, 1969). Wiley (1981) considers a genus "a mandatory category to which every species must belong and which contains one species or a monophyletic group of species". With regard to placing the flexible-rayed redfins in a separate genus of their own there is no conflict with either the traditional or phylogenetic view of that category.

In the case of the redfins there is, however, an important practical difference to be overcome between the evolutionary and phylogenetic approaches. This concerns the generic placement of the species *Oreodaimon quathlambae* which currently commands its monospecific generic status on account of its distinctiveness (Greenwood and Jubb, 1967). In the phylogenetic system adopted here this morphological uniqueness is subsumed within the lineage at the level of common ancestry to the lineage (Wiley, 1981).

There is an available name within the genus group which under Articles 23 and 43 of the International Code of Zoological Nomenclature (3rd edition, 1985) must be used for the flexible-rayed redfin lineage. Andrew Smith (1841) included two species in the sub-genus *Pseudobarbus* (genus *Barbus*)—*B. (Pseudobarbus) burchelli* and *B. (Pseudobarbus) pallidus*. These two species were the first small cyprinids or minnows to be described from southern Africa. The definition of *Pseudobarbus* given by Smith (1841) included the character "intestinal canal long and contorted" which indicates that it was based on *B. burchelli* and not *B. pallidus* because a long coiled gut is a feature only of the former species. In any event there is no contention as to which is the type species of this genus because Jordan (1919) designated *B. burchelli* as the type species of *Pseudobarbus*. A redefinition of the genus *Pseudobarbus* to accommodate all the flexible-rayed redfins and exclude the species *B. pallidus* follows.

Pseudobarbus Smith 1841

Type species : *Pseudobarbus burchelli* Smith 1841, by subsequent designation, Jordan 1919.
Included species: *Pseudobarbus afer* (Peters 1864)
Pseudobarbus asper (Boulenger 1911)
Pseudobarbus burchelli Smith 1841
Pseudobarbus burgi (Boulenger 1911)
Pseudobarbus phlegethon (Barnard 1938)
Pseudobarbus quathlambae (Barnard 1938)
Pseudobarbus tenuis (Barnard 1938)

Diagnosis: Moderate sized (up to 150 mm SL) fusiform or terete cyprinid fishes; snout rounded; mouth sub-terminal or inferior and crescentic or sickle shaped; one or two pairs of simple circum-oral barbels; lips moderately developed sometimes thin and firm; pharyngeal teeth in two or three rows, 0–2, 3, 4–5 + 5–4, 3, 0–2; crowns of pharyngeal teeth variable with an oblique occluding surface with latero-terminal recurved tips (major cusps); intestine variable in length and degree of involution, from a simple single flexure with length sub-equal to SL, to multiple involutions with length up to 3,5 times the SL; peritoneum black. Scales moderately large to very small, radiately striated with radii present in all scale fields; scales on nape irregular and often crowded, reduced or embedded; breast scales reduced and embedded; no elongated trianguloid pelvic axillary scale. Lateral line interrupted or complete, straight or only slightly curved and runs mid-lateral along the caudal peduncle. Cephalic lateral line with preopercular canal not connected to postocular commissure, mandibular canal reduced or absent and supraorbital canal without branches. Adult fish have distinctive bright red patches on proximal half of fins and the adjacent body area. Mature males develop prominent conical tubercles on the snout and dorsal half of the head; small tubercles on the scale margins and bands of tubercles on the upper surface of the pectoral fin rays. Large females may develop tubercle buds or a few poorly developed tubercles on the head. Dorsal and anal fins with three or four simple flexible rays and invariably seven (dorsal) and five (anal) branched fin rays. From five to ten short, thick-set gill rakers on the lower limb (ceratobranchial) of leading gill arch. Total vertebrae 33–40. Supraneural bones absent or vestigial; frontals not overlapping lamellae of supraethmoid; intercalars reduced or absent; exoccipitals with or without a posterior flange; supraorbitals vestigial or short and accommodated in a recess on the supraorbital shelf of the frontal bones; four or five infraorbitals; lachrymal with low dorsal apex; premaxillae short and deep; urohyal with tapered horizontal flange. Pectoral fins sexually dimorphic being larger and more expanded in males;

pectoral girdle stouter in males than females; intramuscular bones vestigial and poorly ossified anterior to the dorsal fin.

SPECIES ACCOUNTS

Pseudobarbus burchelli Smith 1841

Neotype Fig. 36

Synonymy

Barbus (Pseudobarbus) burchelli Smith 1841, page unnumbered, pl XI no. 1. Type locality, "Various rivers of the Cape Colony"; Günther 1868, 96; Gilchrist and Thompson 1913, 417–418 (in part, 2 specimens from Robertson, Cape); Jubb 1965, 26–27, pl VIII; Jubb 1967, 97–99, Fig. 83, pl 14.

?*Barbus gobionides* Valenciennes in Cuvier and Valenciennes 1842, 189.

Gnathendalia vulnerata Castelnau 1861, 57.

Barbus multimaculatus Steindachner 1870, 11–12, Taf III Fig. 2.

Barbus vulneratus Boulenger 1905 b, 45; Boulenger 1911, 148–149 (in part, the 2 specimens from "Zonde Einde River"); Gilchrist and Thompson 1913, 415–416 (in part, Fig. 73 and the specimens from the Zonde Einde River); Barnard 1938 b, 83, Fig. 18 b and c.

Material examined.

Neotype: AMG/P 7223 A, male, 102 mm SL (Fig. 36) collected by S. C. Thorne, 13 December 1978 from the Tradouw River, Breë River system, south west Cape, 33° 56′ 50″ S, 20° 42′ 39″ E. (Under the International Code of Zoological Nomenclature, Art. 75 (f) this locality represents the type locality of the species.)

Other material: a—Breë River system: SAM 4693, Keisers R, Robertson, L. Keet; SAM 17621, Wit R, Bain's Kloof, E. F. Steer; SAM 17422, Tradouw R, K. H. Barnard, October 1925; SAM 18731, Genadendal, K. H. Barnard, January 1937; SAM 18750, Wit R, Bain's Kloof, L. Boonstra, March 1937; SAM 18751, Slanghoek R, K. H. Barnard, March 1937; SAM 18937,

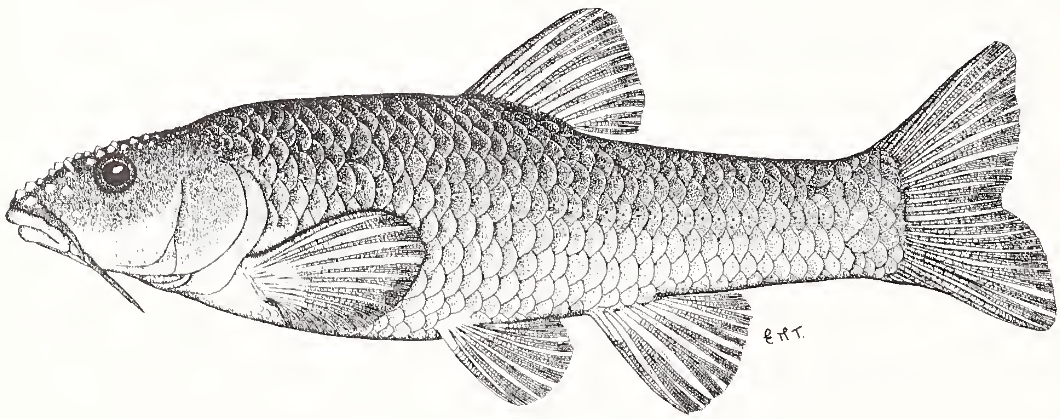

Fig. 36. *Pseudobarbus burchelli* Smith 1841, Neotype, AMG/P 7223A, male, 102 mm SL. Drawn by E. Tarr.

Sonderend R, H. G. Wood, September 1937; SAM 18987, Buffeljags R, K. H. Barnard, February 1938; SAM 22279, Hex R, A. C. Harrison; AMG/P 482, Wit R, Bain's Kloof, R. A. Jubb, November 1960; AMG/P 1411, Wit R, Bain's Kloof, F. L. Farquharson, April 1967; AMG/P 1566, Keisers R, K. H. van Rensburg, December 1967; AMG/P 1791, Keisers R, P. H. Skelton, October 1972; AMG/P 2031, Tradouw R, R. E. Stobbs, 1973; AMG/P 2077, Kabous R, P. H. Skelton, December 1973; AMG/P 2079, Klipplaas R, P. H. Skelton, December 1973; AMG/P 3463 and 3465, Wit R, Bain's Kloof, P. H. Skelton, October 1975; AMG/P 3840, Spreeudrifspruit, I. G. Gaigher, November 1976; AMG/P 4972, Keisers R, C. Stuart, September 1977; AMG/P 5475, Kogmanskloof R, C. Stuart, November 1977; AMG/P 5911–5915, Keisers R, W. C. N. Esterhuizen, 1977–1978; AMG/P 6028, Helderstroom, S. J. McVeigh, June 1978; AMG/P 7205 & 7220, Wit R, S. C. Thorne, February 1979; AMG/P 7223, Tradouw R, S. C. Thorne, December 1978; AMG/P 7224, Slang R, S. C. Thorne, December 1978; AMG/P 7443, Breë R, P. H. Skelton, November 1976; AMG/P 7444, Spreeudrifspruit, P. H. Skelton, November 1976.

b—Kaffirkuils River system: SAM 18988, Vette R, K. H. Barnard, February 1938; AMG/P 7393, Kruis R, S. C. Thorne, December 1978.

c—Duivenhoks River system: SAM 19345, C. K. H. Barnard, October 1938; AMG/P 3472, P. H. Skelton, October 1975; AMG/P 6138, S. C. Thorne, August 1978; AMG/P 7227, S. C. Thorne, December 1978.

d—Kars River: SAM 18979, K. H. Barnard, December 1937.

e—Grashoek River: SAM 18978, K. H. Barnard, December 1937.

f—Nieuwejaars River: SAM 18981, K. H. Barnard, December 1937.

Notes on the taxonomy

The precise identification of Smith's *B. burchelli* is open to debate because no type specimens are known to exist, the original description is entirely qualitative, the given illustration is inaccurate in diagnostic features (Barnard, 1943, and Greenwood and Crass, 1959) and the original locality was only given as "various rivers of the Cape Colony". The present allocation was determined by Jubb (1965) after P. H. Greenwood had examined the type skins of Castelnau's *Gnathendalia vulnerata* and concluded that they agreed with Smith's description of *B. burchelli*. Barnard (1943) previously showed that it was difficult (if at all possible) to determine whether Smith's *B. burchelli* was in fact the Berg River or the Breë River species. Jubb's decision on this species is accepted in the interests of taxonomic stability.

Günther (1868) placed *Gnathendalia vulnerata* in synonymy with *Barbus gobionides* Valenciennes in C and V 1842. Once again no types of the latter species exist and the description is totally inadequate to determine to which species it refers. Barnard (1943) declared the latter species name to be a *nomen dubium*. Boulenger (1905) placed Steindachner's *Barbus multimaculatus* in synonymy with *B. vulnerata* which is in turn now allocated to *P. burchelli*. The types of *B. multimaculatus* in the Natural History Museum of Vienna have been examined and the synonymy is confirmed.

The neotype of *P. burchelli* was selected from well-preserved recently collected material after it was reasonably established that no type(s) of this species have ever been referred to or are known to exist (P. H. Greenwood, pers. comm., and G. Swinney in litt. 1976).

Diagnosis

A redfinned cyprinid minnow reaching 136 mm SL with unbranched dorsal ray flexible, two

pairs of well developed oral barbels each longer than the orbit diameter, breeding males with large conical tubercles on the head, from five to ten on either side of the snout. Intestine involuted up to 2,8 times the SL.

Description

Morphometric proportions and meristic data are given in Table 14. General shape fusiform with predorsal length slightly longer than postdorsal. Head length sub-equal to body depth. Eyes lateral to dorso-lateral. Mouth sub-terminal, protrusible and sickle shaped. Lips moderately developed or retracted from rim of lower jaw. Barbels simple and well developed, in adults both pairs are longer than the orbit diameter.

Scales radiately striate, focus central, radii in all fields. Breast scales are reduced and embedded, nape scales moderately crowded, axil scales of pelvic fin not prominent or elongate.

Paired fins are longer and wider in males, nearly reaching the anterior base of the pelvic fins. In females the shorter pectorals reach to within four or five scales of the pelvic bases. The pelvic fins are fan-shaped, nearly reaching the anterior base of the anal fin in males and to two or three

TABLE 14.

Morphometric and meristic measurements of *P. burchelli* (N=179)

Measurement		*Range* Max.	Min.	$\overline{M}$
Standard length (mm)		136,0	28,0	54,3
Head length (%SL)		33,1	24,7	27,0
Head depth (%HL)		76,8	62,2	69,9
Snout length (%HL)		41,5	30,6	36,0
Orbit diameter (%HL)		36,7	17,8	28,5
Postorbit length (%HL)		50,7	38,5	45,2
Interorbit length (%HL)		36,5	24,1	30,6
Predorsal length (%SL)		55,2	48,9	51,3
Postdorsal length (%SL)		51,4	44,9	48,8
Dorsal fin base (%SL)		15,6	11,2	13,4
Dorsal fin length (%SL)		26,6	19,0	23,2
Pectoral fin length (%SL)		25,0	18,6	21,7
Pelvic fin length (%SL)		19,2	14,0	16,6
Anal fin length (%SL)		25,0	17,3	20,3
Anal fin base (%SL)		13,5	7,1	10,7
Body depth (%SL)		29,3	22,8	25,5
Body width (%SL)		21,8	13,7	16,8
Caudal peduncle length (%SL)		28,0	21,3	24,8
Caudal peduncle depth (%SL)		17,7	10,9	12,3
Anterior barbel length (%OD)		115,0	3,7	55,2
Posterior barbel length (%OD)		166,0	3,7	94,7
Pectoral–pelvic length (%SL)		27,6	21,1	24,6
Pelvic–anal length (%SL)		17,1	11,9	14,3
Pharyngeal bones L/W	(N = 120)	4,5	3,0	3,5
Length of intestine (%SL)	(N = 140)	280,5	73,4	159,2

Meristics	
Dorsal fin rays	iii–iv (iv) + 6–8 (7)
Anal fin rays	iii–iv (iii) + 4–6 (5)
Pectoral fin rays	12–16 (14)
Pelvic fin rays	7–9 (8)
Total vertebrae	34–38 (36–37)
Precaudal vertebrae	17–20 (18–19)
Caudal vertebrae	15–20 (17–18)
Predorsal vertebrae	11–13 (12)
Preanal vertebrae	18–22 (19–20)
Lateral line scales	29–39 (36)
Caudal peduncle scale rows	12–18 (12)
Scale rows lat. line –dorsal	5–7 (6)
Scale rows lat. line –pelvic	4–6 (4)
Scale rows lat. line –anal	4–6 (4)
Predorsal scale rows	14–22 (17–19)
Primary scale radii ($\overline{M}$ to nearest whole no.)	10
Pharyngeal teeth (mode)	2, 3, 5–5, 3, 2

scales before this fin in females. The posterior edge of the dorsal and anal fins is straight or gently rounded. The anterior base of the dorsal fin lies just posterior to the origin of the pelvic fins. The caudal fin is forked with rounded lobes.

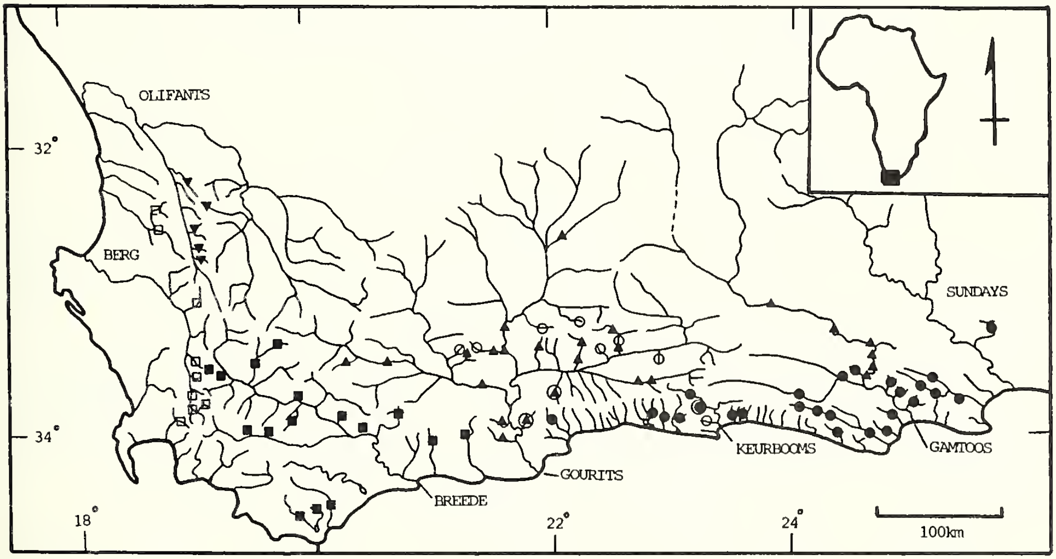

Fig. 37 A. Distribution of *Pseudobarbus* species in Cape coastal river systems based on museum records referred to in this study. Symbols may include multiple collection records. Unshaded square—*P. burgi*, shaded square—*P. burchelli*, inverted shaded triangle—*P. phlegethon*, shaded triangle *P. asper*, unshaded circle—*P. tenuis*, shaded circle—*P. afer*.

There are 2–3 + 6–9 short gill rakers on the leading arch. The pharyngeal bones are falcate with three rows of teeth in the formula 2, 3, 5–5, 3, 2. Pharyngeal teeth have obliquely truncate crowns which are closely applied to each other to form a grinding occlusal surface. The intestine is involuted with two or three secondary coils and extends up to 2,8 times the SL.

Mature sexually active males develop large conical tubercles on the top of the head and the snout. At full development the pattern includes bilateral groups of five to ten tubercles on the snout, single arcs above the nares and orbits and scattered tubercles on the head dorsum. Bands of small tubercles from five to six deep develop over the branched pectoral fin rays. Single tubercle rows occur on the rays of other fins. A single row of minute tubercles forms along the free edge of body scales. Large mature and sexually active females develop tubercle buds on the head.

Colour variable, from light to dark olive green or brown in juveniles becoming darker in adults. Juveniles with large dark blotches along the flanks and over the dorsal half of the body including a mid-lateral series of irregular spots with a large sub-triangular mark at the end of the caudal peduncle. Basal half of fins scarlet in mature fishes, fin rays dark brown, the membranes hyaline distally.

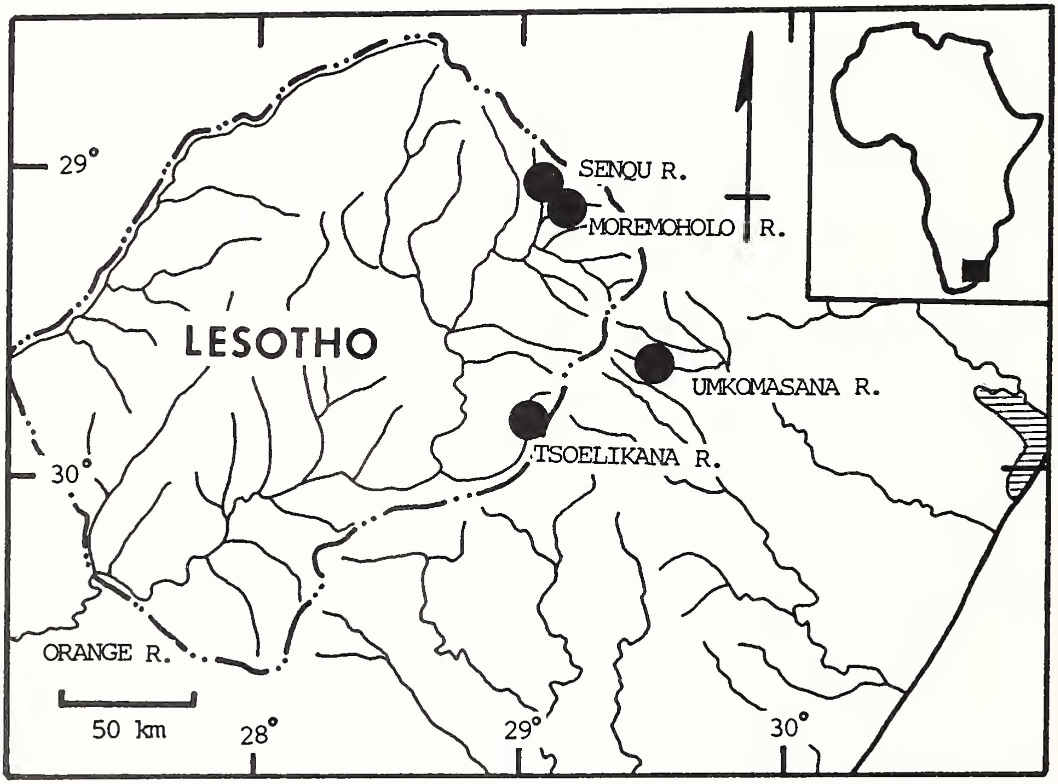

Fig. 37 B. The distribution of *P. quathlambae* in tributaries of the Orange (Senqu) River in Lesotho and the Umkomazana River in Natal, based on museum records referred to in this study. Symbols may include multiple collection records.

The lateral line is complete or semi-complete, and passes more-or-less mid-laterally along body and caudal peduncle. Cephalic lateral line with a disjunct preopercular-mandibular canal which is reduced from the anterior end of the mandible.

Distribution

P. burchelli is found throughout the Cape Fold Mountains reaches of the Breë River system as well as the adjacent Kars, Nieuwejaars and Sout river systems to the west and the Duivenhoks and Kaffirkuils rivers to the east (Fig. 37A). In a recent study Cambray and Stuart (1985) found that the species was virtually absent from the mainstream of the Breë River and tended to exist only in tributaries of the system.

Conservation status

Burchell's redfin is included in the South African Red Data Book—Fishes as a rare species (Skelton, 1987).

Etymology

The species was named for the naturalist and early explorer-traveller in South Africa, William Burchell.

Pseudobarbus burgi (Boulenger 1911)

Fig. 38.

Synonymy

Barbus anoplus (*non* Weber 1897, 152 (in part, the specimen from Frenchhoek).

Barbus burchelli: Boulenger 1911, 164, Fig. 122 (in part, the Eerste River specimens); Gilchrist and Thompson 1917, 417–418, Fig. 75 (in part, the Eerste River and Berg River specimens); Barnard 1938 b, 82–83; Barnard 1943, 185–188, Fig. 18a.

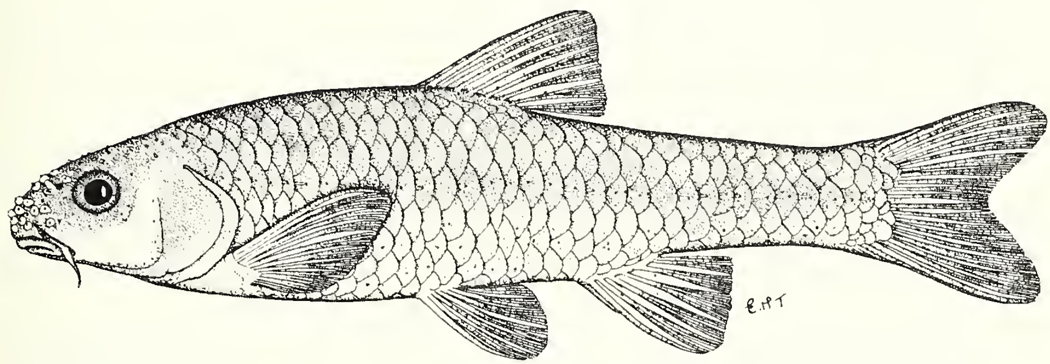

Fig. 38. *Pseudobarbus burgi* (Boulenger 1911), AMG/P 6156, male, 85 mm SL, Drawn by E. Tarr.

Barbus burgi Boulenger 1911, 147–148, Fig. 124. Type locality "Burg (*sic*) River, Paarl division"; Gilchrist and Thompson 1917, 419, Fig. 76; non Pellegrin 1936, 55.
Barbus afer (*non* Peters 1864); Boulenger 1911, 178–179.
Barbus bergi: Jubb 1965, 27–28, Fig. 9 (unjustified emendation); Jubb 1967, 99, Fig. 84.

Material examined

Lectotype: BMNH 1901.2.11.14, 72 mm SL, collected by Mr Brown from the Berg River, Paarl division. Paralectotypes: BMNH 1901.2.11.15–16, 67 mm and 61 mm SL, collected with the holotype.

Other material: a—Berg River system : SAM 4696, Paarl, Mr Brown; SAM 18094, Groot Drakenstein, A. C. Harrison, 1930; SAM 18608, Lemiet R, K. H. Barnard, 1936; SAM 18747, Groot Drakenstein, K. H. Barnard, 1937; SAM 19027, Bushmans R, K. H. Barnard, September 1938; SAM 18935, Twentyfour R, K. H. Barnard, August 1937; AMG/P 1578, 1579, Krom R, C. M. Gaigher, February 1971; AMG/P 2076, Krom R, P. H. Skelton, December 1973; AMG/P 4041, Wemmershoek, P. H. Skelton, June 1977; AMG/P 6144, 6148, Franschoek R, S. C. Thorne, November 1978; AMG/P 6153, 6156, Wemmershoek, S. C. Thorne, November 1978; AMG/P 6170, Wemmers R, S. C. Thorne, November 1978; AMG/P 7211, Boesmans R, S. C. Thorne, February 1979.

b—Eerste River: SAM 4695, Peringuey; SAM 5090, Dr Kruger; SAM 22746, Stellenbosch dam, A. C. Harrison; TM 8348 (779), Stellenbosch dam, Dr van der Horst, Oct 1930; BMNH 1901.2.11.11–13, Eerste R, at Stellenbosch, donated by the SAM.

c—Verlorevlei River: AMG/P 1874, Berg Valley stream, P. H. Skelton, February 1973; AMG/P 1875, Kruis R, P. H. Skelton, February 1973.

Notes on the taxonomy

The close similarity between *P. burgi* and *P. burchelli* and the confusion in the identity of the latter species has affected the nomenclatural history of both species. Barnard (1938b) placed *B. burgi* as a junior synonym of *B. burchelli* recognising the Breë River species as *B. vulneratus*. Jubb (1965) switched the arrangement by naming the Breë River species as *B. burchelli* with *B. vulneratus* as its junior synonym and calling the Berg River species *B. burgi* (his emendation of the spelling to *bergi* is unjustified and hence rejected here). Although, in the author's opinion, the evidence for this switch is equivocal, and therefore is dubiously justified (see taxonomic history above), to reverse the decision at this stage would simply cause further confusion and is equally unjustified.

The specimen from the Okavango River identified as *B. burgi* by Pellegrin (1936) is not of this species (Skelton, pers. obs.) (*vide* Barnard, 1943).

The lectotype was chosen from the syntype series of three specimens on the basis of size and condition. The specimens of the type series were originally derived from a sample in the SAM (SAM 4696).

Diagnosis

Unbranched dorsal ray is slender and flexible; two pairs of simple oral barbels, the anterior pair is short and is only present in specimens above 40 mm SL (i.e. adults and sub-adults); pharyngeal teeth with truncate oblique crowns; intestine involuted but variable, up to 3,6 times the SL; mature males with large conical tubercles on the head, at full development there are from 10 to 15 clustered on either side of the snout. Most similar to *P. burchelli* from which it is

distinguished by having slightly larger scales (30–35 *vs* 32–37 in the lateral line), shorter anterior barbels, a slightly more anterior placement of the dorsal fin, the smaller more numerous tubercles on the head, and a more expansive 5th infraorbital.

Description

Morphometric and meristic data are given in Table 15. A medium sized (reaches 109 mm SL) fusiform cyprinid minnow. Head deep with rounded anterior profile, its length sub-equal to the depth of the body. Eyes lateral. Mouth sickle-shaped, inferior and protrusible, with moderate lips and two pairs of simple barbels.

Body with radiately striated scales, radii from central focus in all of the scale fields. Breast scales reduced and embedded, isthmus area naked. There are no elongated pelvic axillary scales.

The dorsal fin originates above the pelvics, the posterior edge of dorsal and anal fins more-or-less straight; the caudal fin is forked with rounded lobes. The paired fins are sexually

TABLE 15.

Morphometric and meristic measurements of *P. burgi* (N=107)

Measurement		*Range*		
		Max.	Min.	$\overline{M}$
Standard length (mm)		109,0	34,0	59,4
Head length (%SL)		29,4	22,9	25,9
Head depth (%HL)		80,8	64,0	73,8
Snout length (%HL)		42,1	30,0	35,6
Orbit diameter (%HL)		37,5	22,3	29,1
Postorbit length (%HL)		53,0	38,7	47,1
Interorbit length (%HL)		40,0	27,8	33,5
Predorsal length (%SL)		53,8	44,6	48,9
Postdorsal length (%SL)		55,4	46,3	51,1
Dorsal fin base (%SL)		15,4	11,7	13,7
Dorsal fin length (%SL)		28,4	16,1	24,5
Pectoral fin length (%SL)		26,4	14,7	21,5
Pelvic fin length (%SL)		20,7	7,9	17,9
Anal fin length (%SL)		23,4	14,0	20,1
Anal fin base (%SL)		12,4	8,5	10,3
Body depth (%SL)		32,0	20,9	27,4
Body width (%SL)		18,6	9,8	15,2
Caudal peduncle length (%SL)		38,3	20,9	25,0
Caudal peduncle depth (%SL)		3,3	9,1	11,8
Anterior barbel length (%OD)		80,0	2,8	18,7
Posterior barbel length (%OD)		47,3	21,9	71,2
Pectoral–pelvic length (%SL)		32,0	16,5	24,7
Pelvic–anal length (%SL)		21,1	13,0	15,8
Pharyngeal bones L/W	(N = 58)	4,2	2,7	3,3
Length of intestine	(N = 81)	360,6	116,9	231,7

Meristics

Dorsal fin rays	iii–iv (iii) + 6–8 (7)
Anal fin rays	ii–iv (iii) + 5–6 (5)
Pectoral fin rays	13–18 (14–15)
Pelvic fin rays	7–9 (8)
Total vertebrae	35–39 (36–37)
Precaudal vertebrae	17–20 (19)
Caudal vertebrae	16–20 (18)
Predorsal vertebrae	10–12 (11–12)
Preanal vertebrae	19–21 (20)
Lateral line scales	28–37 (30–34)
Caudal peduncle scale rows	12–16 (12)
Scale rows lat. line –dorsa	4–6 (5)
Scale rows lat. line –pelvic	3–5 (4)
Scale rows lat. line –anal	3–5 (4)
Predorsal scale rows	12–18 (15)
Primary scale radii ($\overline{M}$ to nearest whole no.)	8
Pharyngeal teeth (mode)	2, 3, 5–5, 3, 2

dimorphic with males having larger more expansive and rounded pectorals and pelvics than the females.

The gill rakers are short and stubby with 2–4 + 6–10 on the leading arch. Pharyngeal bones are falcate with teeth in 3 rows in the formula 2, 3, 5–5, 3, 2. Pharyngeal teeth have obliquely truncate closely applied crowns that present a grinding-type occlusal surface. The intestine is involuted with two or three secondary coils and extends up to 3,5 times the SL in adults from certain populations.

Conspicuous conical tubercles develop on the head of sexually active males. The pattern of these tubercles is similar to that of *P. burchelli* but the tubercles are relatively smaller and more numerous in relation to those of the latter species. There can be from 10–15 tubercles in separate bi-lateral clusters on the snout. Tubercle bands with three or four tubercles across overlie the pectoral fin branched rays. Single rows of tubercles occur on the rays of the other fins. A single arc of tubercles occurs along the free edge of each scale in all but the most ventral (belly) region of the body. Large females develop a few tubercle buds on the head.

Colour varies with habitat from light brown to dark olive, flanks may be silvery with ventral parts light greyish cream. Fins hyaline in juveniles becoming scarlet red over basal part in adults. A dark irregular lateral band that ends in the form of a sub-triangular mark at the base of the caudal fin is more prominent in juveniles. Fine parallel longitudinal lines above the lateral band are also variously present in preserved specimens. The iris is silvery golden, the operculum iridescent golden.

The lateral line passes straight along the body and is complete or semi-complete. The cephalic lateral line system has a disjunct preopercular-mandibular canal and the mandibular portion is reduced from the anterior end to form a short canal which just reaches the dentary bone. The 5th infraorbital bone is relatively well developed with broad flanges.

Distribution

Pseudobarbus burgi occurs in the Verlorevlei River system, the Great Berg River system

and formerly in the Eerste River (last known record in 1930, however, Barnard (1943) stated that the species was still present in the system at that time) (Fig. 37A). The range of the species has been severely reduced in the Great Berg River system over the past few decades and the species is now restricted to a few small tributaries.

Conservation status

The Berg River redfin is an endangered species (Skelton, 1987).

Etymology

This species was named for the Great Berg River, south west Cape.

Pseudobarbus phlegethon (Barnard 1938)

Fig. 39.

Synonymy

Barbus phlegethon Barnard 1938 b, 87–88. Type locality "Olifants River, Clanwilliam, Cape"; Barnard 1943, 204–206, Fig. 20; Jubb 1965, 32, Fig. 13; Jubb 1967, 97, Fig. 82.

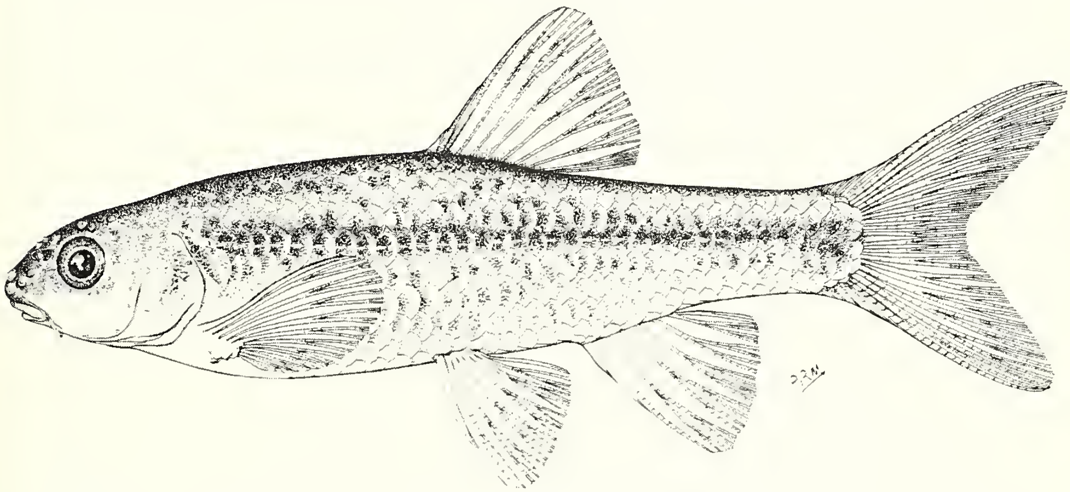

Fig. 39. *Pseudobarbus phlegethon* (Barnard 1938), AMG/P 8203, male, 50 mm SL. Drawn by P. Meakin.

Material examined

Lectotype: SAM 22484, male, 43 mm SL; 32 paralectotypes SAM 22484 (this is a composite sample derived from SAM 18767 and SAM 19003, see taxonomic notes); 25 paralectotypes SAM 18767 Boontjies River, Olifants River system, K. H. Barnard, April 1937; 29 paralectotypes SAM 19003 Boontjies River, Olifants River system, K. H. Barnard, April 1938.

Other material: all Olifants River system : SAM 22479, Thee R, K. H. Barnard; SAM 22483, K. H. Barnard, February 1939; AMG/P 722, Thee R, K. van Rensburg, January 1964; AMG/P 1394, Keerom, K. van Rensburg, January 1964; AMG/P 1399, Noordhoeks R, F. L.

Farquharson, April 1967; AMG/P 1820 and 1821, Thee R, D. Heard, September 1972; AMG/P 1852, Jan Diessels R, P. H. Skelton, January 1973; AMG/P 1863, Noordhoeks R, P. H. Skelton, February 1973; AMG/P 1868, Thee R, P. H. Skelton, February 1973; AMG/P 1880, Noordhoeks R, K. van Rensburg, March 1965; AMG/P 2053, Noordhoeks R, P. H. Skelton, October 1973; AMG/P 2054, Driehoek R, P. H. Skelton, October 1973; AMG/P 7366, Driehoek R, P. H. Skelton, December 1978.

Notes on the taxonomy

Dr K. H. Barnard was not meticulous in designating or labelling type material and consequently there is sometimes doubt as to what constitutes the type material of the species he described. In the absence of information to the contrary the author regards the type material of Barnard's species as that material known to have been available to him before the publication of the species description. In the case of *P. phlegethon* the samples concerned are SAM 18767 and SAM 19003 which were combined at some time prior to the present revision, labelled as syntypes and given the new accession number SAM 22484 (Dr P. A. Hulley SAM, in litt., November 1979). The lectotype was selected from this series on the basis of size and condition.

Diagnosis

A moderately small cyprinid (maximum size recorded 71 mm SL), with a small inferior mouth and a single pair of short oral barbels. The pigmentation is a striking combination of black blotches on a lighter brown and silvery white background. The species is not easily confused with other cyprinid species in the Olifants system on account of its small mouth and short single pair of barbels. There are five branched rays in the anal fin.

Description

The morphometric and meristic data for this species are given in Table 16. The general shape is fusiform with head length sub-equal to the bodydepth. The head is compressed with an ovoid lateral profile. The eyes are lateral. The mouth is sub-terminal, protrusible and sickle-shaped. The lips are moderately well developed or retracted from the rim of the mandible. The gill openings are attached at the isthmus. There is a single pair of short barbels at the angle of the mouth.

The body is moderately compressed, the length of the caudal peduncle is greater than twice the depth. Scales are cycloid with radiate striae in all fields. Breast scales are reduced in size and embedded and there are no triangular scales in the axils of the pelvic fins.

The paired fins are dimorphic in the sexes with mature males having longer, more rounded and expansive pectorals and pelvic fins than the females. The pectorals almost reach the base of the pelvics in the males and their pelvics reach the base of the anal. The hind edge of the dorsal and anal fins is nearly straight or slightly concave. The caudal fin is forked with pointed lobes. The dorsal fin originates above or just behind the origin of the pelvic fins.

There are 2 + 4–6 short, blunt gill rakers on the leading arch. The pharyngeal bones are falcate with a length to width ratio of 2,9–3,9. The pharyngeal teeth occur in three rows, 1, 3, 5–5, 3, 1. The crowns of the pharyngeal teeth are obliquely truncate. The intestine is involuted and up to 2,5 times the SL.

Mature breeding males have few small conical tubercles on the snout and on top of the head. There are bands of minute tubercles over the pectoral branched fin rays. Tubercles have not been observed on the scales of this species.

TABLE 16.

Morphometric and meristic measurements of *P. phlegethon* (N=92)

Measurement		*Range* Max.	Min.	$\overline{M}$
Standard length (mm)		59,5	27,5	43,3
Head length (%SL)		28,7	23,9	25,6
Head depth (%HL)		82,4	66,9	75,0
Snout length (%HL)		41,2	31,1	35,2
Orbit diameter (%HL)		36,3	25,3	30,2
Postorbit length (%HL)		57,1	43,1	46,4
Interorbit length (%HL)		38,8	27,2	32,8
Predorsal length (%SL)		55,2	49,0	52,4
Postdorsal length (%SL)		51,0	44,8	47,6
Dorsal fin base (%SL)		15,2	10,9	13,3
Dorsal fin length (%SL)		27,6	19,2	24,0
Pectoral fin length (%SL)		25,3	17,8	20,9
Pelvic fin length (%SL)		20,8	15,4	17,3
Anal fin length (%SL)		23,7	17,0	21,2
Anal fin base (%SL)		12,1	9,1	10,1
Body depth (%SL)		27,8	21,4	24,2
Body width (%SL)		17,6	11,7	14,4
Caudal peduncle length (%SL)		26,9	21,4	23,9
Caudal peduncle depth (%SL)		12,1	9,1	10,8
Anterior barbel length (%OD)		—	—	—
Posterior barbel length (%OD)		50,0	2,6	26,9
Pectoral–pelvic length (%SL)		31,9	23,3	27,4
Pelvic–anal length (%SL)		18,9	12,0	14,7
Pharyngeal bones L/W	(N = 63)	3,9	2,9	3,4
Length of intestine (% SL)	(N = 77)	244,0	78,1	142,4

Meristics	
Dorsal fin rays	iii–iv (iii) + 6–8 (7)
Anal fin rays	iii–iv (iii) + 5–6 (5)
Pectoral fin rays	11–15 (13–14)
Pelvic fin rays	7–9 (8)
Total Vertebrae	35–37 (36)
Precaudal vertebrae	17–19 (18)
Caudal vertebrae	16–19 (17–18)
Predorsal vertebrae	11–14 (12–13)
Preanal vertebrae	18–21 (20)
Lateral line scales	29–37 (35)
Caudal peduncle scale rows	10–14 (12)
Scale rows lat. line–dorsal	4–6 (5)
Scale rows lat. line–pelvic	3–4 (4)

Meristics

Scale rows lat. line–anal	3–5 (3–4)
Predorsal scale rows	14–20 (16–17)
Primary scale radii ($\overline{M}$ to nearest whole no.)	12
Pharyngeal teeth (mode)	1, 3, 5–5, 3, 1

Small fry and juveniles of the species have a single dark lateral stripe from behind the head to the base of the caudal fin. Adult specimens are heavily blotched with irregular black spots on the body apart from the ventral belly region. The background colour is a light brown with silvery-white lower flanks and belly. The head is darker above and light below with the cheek and opercular regions silvery golden. The iris of the eyes is also golden. The fin membranes are hyaline distally and brilliant red over the basal portions, especially in ripe breeding males. The fin rays are brown with the fork of the branched rays darker brown or black giving a banded effect.

The lateral line runs straight from the head to the base of the caudal fin and is generally complete. The cephalic lateral line is disjunct at the dorsal or posterior end of the pre-opercular branch. The mandibular canal is completely absent.

As with other *Pseudobarbus* species the supraneural bones are vestigial or absent and the anterior epipleurals are reduced and poorly ossified. The neurocranium of this species is relatively narrow and deep and the hyomandibular has short dorso-anterior projections.

Distribution

Pseudobarbus phlegethon is endemic to the Clanwilliam Olifants River system (Fig. 34). Within the system it is confined to clear water tributaries of the valley mainstream with only a single population known from the eastern drainage of the Cedarberg mountains (the Driehoek River). Valley tributaries where the species has been collected include the Ratels, the Oudste, the Thee, the Noordhoeks, the Boontjies and the Jan Diessels.

Notes on biology

Underwater observations on this species in the Noordhoeks River on the 7 January 1981 (Skelton, pers. obs.) indicate that mature males in ripe-running breeding condition are territorial.

Conservation status

The fiery redfin is an endangered species (Skelton, 1987).

Etymology

The name "phlegethon" is taken from the mythical fiery river of the underworld and refers to the heat of the Clanwilliam Olifants River valley during summer (Jubb, 1965).

Pseudobarbus tenuis (Barnard 1938)

Fig. 40.

Synonymy

Barbus anoplus (non Weber): Gilchrist and Thompson 1913, 428 (in part, specimens from the Le Roux River).

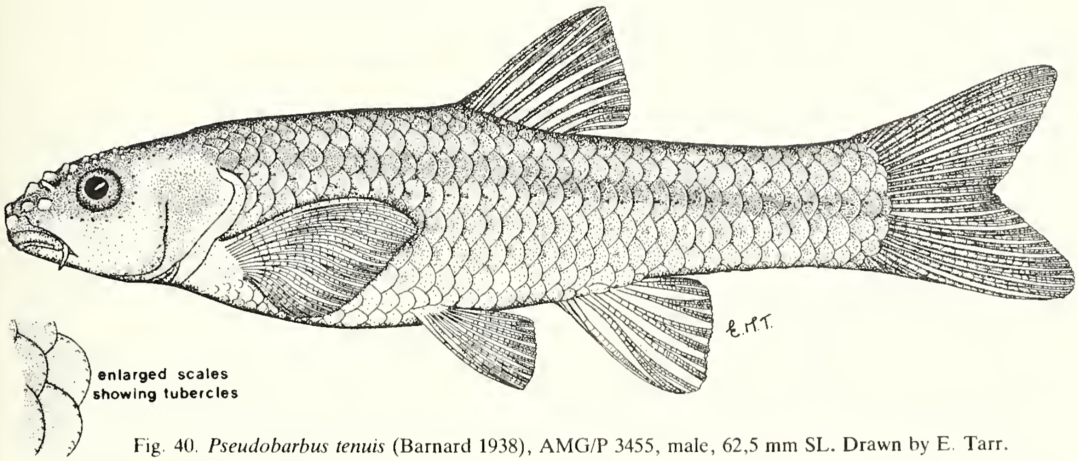

Fig. 40. *Pseudobarbus tenuis* (Barnard 1938), AMG/P 3455, male, 62,5 mm SL. Drawn by E. Tarr.

Barbus tenuis Barnard 1938, 87, type locality "Gouritz River system"; Barnard 1943, 202–204, Fig. 19b; Jubb 1965, 31, Fig. 12; Jubb 1967, 101, Fig. 87; Skelton 1976, Fig. 10b.

Material examined

Lectotype: SAM 18953, female, 74 mm SL, collected by K. H. Barnard, C. W. Thorne and A. C. Harrison from between De Rust and Rust-en-Vrede (probably the Nels River) on the 24 October 1937.

Paralectotypes: SAM 18953, 313 specimens, collected with the lectotype; (SAM 10667, 3 specimens, Le Roux River); SAM 18946, 220 specimens, Seven Weeks Poort, K. H. Barnard, October 1937; SAM 18969, 192 specimens, Grobbelaars River, K. H. Barnard, 24 October 1937;(SAM 18970, Langtouw River, K. H. Barnard, 26 October 1937).

Other material: a—Gourits River system: BMNH 1938.2.28:7–8, tributary of Olifants R, (Gourits system), K. H. Barnard; SAM 19535, Waterval R, Kammanassie, K. H. Barnard, January 1940; SAM 22332, Moeras R; AMG/P 608, Meiringspoort, R. A. Jubb, October 1961; AMG/P 1569, Meiringspoort, C. M. Gaigher, November 1970; AMG/P 1587, Waterkloof R, C. M. Gaigher, May 1971; AMG/P 1935, Wilge R, P. H. Skelton, April 1973; AMG/P 2081, Wilge R, P. H. Skelton, December 1973; AMG/P 2664, Rusoord, P. H. Skelton, January 1975; AMG/P 2666, Waterkloof R, P. H. Skelton, January 1975; AMG/P 2667, Kruis R, P. H. Skelton, January 1975; AMG/P 2945, Meiringspoort, R. A. Jubb, November 1960; AMG/P 2946, Meiringspoort, R. A. Jubb, October 1960; AMG/P 3455, Wilge R, P. H. Skelton, October 1975; AMG/P 4288, Meiringspoort, M. Currey, March 1977; AMG/P 4809 Bo-Buffelskloof, S. Rudd, April 1977; AMG/P 4920, Seven Weeks Poort, R. Boycott, January 1977; AMG/P 6030, Kruis R, S. C. Thorne, August 1978; AMG/P 6031, 6032,6036, 6038, Nels R, S. C. Thorne, August 1978; AMG/P 6060, Groot R, S. C. Thorne, August 1978; AMG/P 6063, 6064,6067, 6071, Meiringspoort, S. C. Thorne, August 1978; AMG/P 6081, 6082, Le Roux R, S. C. Thorne, August 1978; AMG/P 6121, Seven Weeks Poort, S. C. Thorne, August 1978; AMG/P 6161, Jan Muller Bridge, S. C. Thorne, August 1978.

b—Keurbooms River System: AMG/P 2944, Diep R, P. H. Skelton, September 1972; AMG/P 3462, Diep R, P. H. Skelton, October 1975; AMG/P 3822, Bitou R, D. Heard, October

1976; AMG/P 3824, Diep R, D. Heard, October 1976; AMG/P 3825, Voogste R, D. Heard, October 1976.

Notes on the Taxonomy

Jubb (1965) gave the type material of *B. tenuis* as lost. As noted above, the present author considers that the material available to Dr Barnard prior to the publication of the original description represents the type material. Therefore the type material of *P. tenuis* is considered to include the following samples SAM 10667, SAM 18946, SAM 18953, SAM 18969 and SAM 18970. Of these only SAM 18946, SAM 18953 and SAM 18969 have been traced. A lectotype has been selected from SAM 18953 which was collected from between De Rust and Rust-en-vrede (probably the Nels River) on 24 October 1937 by Dr K. H. Barnard, C. W. Thorne and A. C. Harrison.

Diagnosis

A terete redfin minnow with the length of the head greater than the depth of the body. A single pair of relatively short barbels (less than the orbit diameter). The pharyngeal teeth in two rows only 3, 5–5, 3. The intestine short, up to 1,3 times the SL with a single major flexure and slight secondary involutions in large specimens. The pelvic fins have seven rays only. In addition to these characters *P. tenuis* is distinguished from *P. afer* and *P. asper* by the pigment pattern (especially the bold mid-dorsal stripe) and the greater number of striae on the scales.

Description

The morphometric and meristic measurements of *P. tenuis* are given in Table 17. The species is more slender than other redfins and has a terete body shape. The head length is greater than the body depth and the lateral head profile is acutely rounded. The eyes are dorso-lateral in position and are not generally visible from below. The protrusible mouth is sickle-shaped and inferior, with moderately developed lips. There are single short simple barbels at the angles of the mouth. The gill openings are attached at the isthmus.

TABLE 17.

Morphometric and meristic measurements of *P. tenuis* (N=96)

Measurement	*Range*		
	Max.	Min.	$\overline{M}$
Standard length (mm)	80,0	30,0	
Head length (%SL)	30,0	24,6	26,7
Head depth (%HL)	71,2	61,1	65,9
Snout length (%HL)	42,4	30,7	35,0
Orbit diameter (%HL)	30,2	20,6	26,0
Postorbit length (%HL)	54,4	43,7	47,5
Interorbit length (%HL)	35,7	25,3	30,1
Predorsal length (%SL)	54,6	48,3	51,4
Postdorsal length (%SL)	51,7	45,5	48,6
Dorsal fin base (%SL)	14,3	11,0	12,6
Dorsal fin length (%SL)	28,0	19,7	22,8

Measurement		*Range* Max.	Min.	$\overline{M}$
Pectoral fin length (%SL)		24,3	16,7	21,0
Pelvic fin length (%SL)		18,1	10,9	15,8
Anal fin length (%SL)		24,1	16,9	20,1
Anal fin base (%SL)		12,9	8,2	10,4
Body depth (%SL)		26,8	18,8	22,4
Body width (%SL)		20,4	13,3	16,6
Caudal peduncle length (%SL)		29,2	23,1	26,3
Caudal peduncle depth (%SL)		21,1	10,5	12,3
Anterior barbel length (%OD) (N = 8)		27,8	7,7	16,8
Posterior barbel length (%OD)		100,0	20,0	68,1
Pectoral–pelvic length (%SL)		28,5	22,4	25,3
Pelvic–anal length (%SL)		18,2	12,5	14,5
Pharyngeal bones L/W	(N = 72)	4,6	3,1	3,8
Length of intestine (%SL)	(N = 23)	133,9	77,1	103,3

Meristics	
Dorsal fin rays	iii–iv (iii) + 6–8 (7)
Anal fin rays	iii–iv (iii) + 5–6 (5)
Pectoral fin rays	12–16 (14)
Pelvic fin rays	7–8 (7)
Total Vertebrae	33–38 (36–37)
Precaudal vertebrae	17–19 (18)
Caudal vertebrae	16–19 (18)
Predorsal vertebrae	11–13 (12)
Preanal vertebrae	17–20 (19)
Lateral line scales	32–37 (35–36)
Caudal peduncle scale rows	11–16 (12)
Scale rows lat. line–dorsal	4–6 (5)
Scale rows lat. line–pelvic	3–5 (4)
Scale rows lat. line–anal	3–5 (4)
Predorsal scale rows	14–22 (16)
Primary scale radii ($\overline{M}$ to nearest whole no.)	14
Pharyngeal teeth (mode)	3, 5–5, 3

The body is rounded or slightly depressed in transverse section with the caudal peduncle usually slightly more than twice as long as deep. The scales are cycloid with a mode of 14 primary radial striae from a central focus in all scale fields. The breast scales are reduced and embedded, the scales on the nape are either absent or reduced and crowded, there are no triangular pelvic axillary scales.

In males the paired fins are longer, more rounded and expansive than in the females. The pectorals reach the base of the pelvics and the pelvics reach the anterior base of the anal in males. The posterior edge of the dorsal and anal fins is straight or only slightly convex. The

caudal fin is forked with obtusely rounded lobes. The dorsal fin originates behind (posterior to) the origin of the base of the pelvic fins.

The gill rakers are short with 2–3 + 5–8 on the anterior arch. The pharyngeal bones are falcate with a length to width ratio of 3–4,5. There are two rows of pharyngeal teeth, 3, 5–5, 3. The pharyngeal teeth have oblique crowns with single recurved pointed cusps. The intestine is reflexed in a single coil with shallow secondary involutions in larger specimens.

Mature breeding males develop large conical tubercles on the head with a similar pattern to that described in detail for *P. burchelli*. In well developed series there are clusters of up to four or five tubercles on either side of the midline on the snout. Single rows of small tubercles develop over the pectoral branched rays, as well as along the free edge of the body scales.

The colour is basically an olive brown above with lighter underparts with the intensity and particular shade depending on the environment. The pigment pattern of *P. tenuis* is distinctive with a prominent mid-dorsal stripe, which may be interrupted, running from the nape to the dorsal fin and continuing behind the dorsal fin to the base of the caudal. A single mid-lateral band runs on either side from behind the head to the base of the caudal fin. The proximal portion of the fins is scarlet in adult fishes, the fin rays are light brown and the distal membranes hyaline. The iris of the eye is golden and the opercles are metallic silvery-gold.

The lateral line is complete and runs more-or-less straight along mid-body to the end of the caudal peduncle. The cephalic lateral line network lacks a mandibular portion and the preopercular canal is disjunct from the post-ocular commissure.

The neurocranium of this species is relatively broad and shallow and anterior bones are lightly ossified. The hyomandibular is elongated and the supraorbitals are small or vestigial. The supraneurals are vestigial or absent.

Distribution

P. tenuis is found in both the Gourits and the Keurbooms River systems. In the Gourits the species is restricted to tributaries of the Cape Fold Mountains and is not encountered in the lowland mainstreams.

Conservation status

The slender redfin is listed as a rare species in the South African Red Data Book, Fishes (Skelton, 1987).

Etymology

The name *tenuis* refers to the relatively slender profile of the species.

Pseudobarbus afer (Peters 1864)

Fig. 41.

Synonymy

Barbus (Capoeta) afer Peters 1864, 395, Type locality: "Cap der guten Hoffnung"; Günther 1868, 148; non Boulenger 1911, 178, Fig. 156; non Gilchrist and Thompson 1913, 430, Fig. 88; Barnard 1938b, 85; Barnard 1943, 217; Jubb 1965, 29–30, Fig. 11; Jubb 1967, 101, Fig. 88.

Barbus anoplus (non Weber 1894): Boulenger 1911, 177, Fig. 155 (in part, the specimens from the Baakens River, Port Elizabeth); Gilchrist and Thompson 1917, Fig. 87.

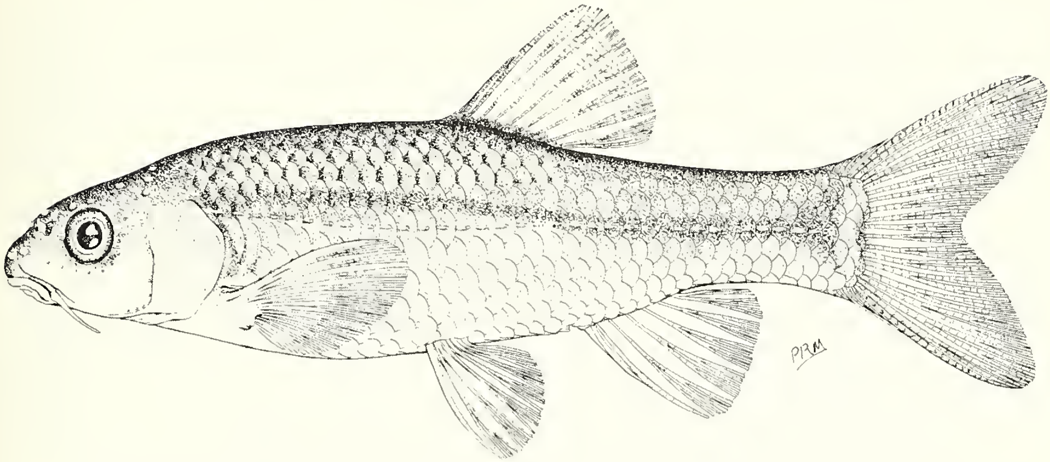

Fig. 41. *Pseudobarbus afer* (Peters 1864), AMG/P 9514, male, 62 mm SL. Drawn by P. Meakin.

Barbus vulneratus (non Castelnau 1861): Gilchrist and Thompson 1913, 415–416 (in part, specimens from the Baakens and Swartkops Rivers).
Barbus senticeps Smith 1936, 266–267, Fig. 3; Smith 1937, 124–125, Fig. 2; Barnard 1938b, 84; Barnard 1943, 200–202.
Barbus asper (non Boulenger 1911): Barnard 1943, 196–200 (in part, specimens listed under (b) and (c) on p.197); Jubb 1965, 28–29, Fig. 10, pl. VIII (in part, specimens from localities other than the Gourits River system and the Groot River, Gamtoos River system); Smith and Smith 1966, 154, Fig. unnumbered.

Material examined

a—Sundays River system, all from the Wit River tributary: AMG/P 455, R. A. Jubb, April 1959; AMG/P 586, R. A. Jubb, 1960; AMG/P 755, R. A. Jubb, April 1959; AMG/P 1188, B. Donnelly, February 1965; AMG/P 3843, P. H. Skelton, December 1976; AMG/P 7465, P. H. Skelton, December 1977.

b—Swartkops River system: SAM 18592, Swartkops R, C. L. Biden, 1935; SAM 19208, Groendal R, C. W. Thorne, October 1938; SAM 19212, Swartkops R; SAM 22330, Swartkops R, Arense; SAM 22334, Swartkops R; AMG/P 675, Elands R, R. A. Jubb, February 1964; AMG/P 2524, Elands R, P. H. Skelton, September 1974; AMG/P 3786, Bulk R, D. Heard, October 1976.

c—Baakens River: SAM 10654, PE Museum, pre-1913; AMG/P 776, D. Bickell, January 1964; AMG/P 1810, P. H. Skelton, November 1972.

d—Maitlands River: AMG/P 5835, A. Bok, January 1978.

e—Gamtoos River system: SAM 19216, Loerie R, C. W. Thorne, October 1938; SAM 19319, Patensie, C. W. Thorne, October 1938; SAM 19496, Baviaanskloof R, K. H. Barnard, April 1939; AMG/P 473, Baviaanskloof R; AMG/P 676, Loerie R, F. L. Farquharson, 1964; AMG/P 712, Moordenaars R, R. A. Jubb, February 1958; AMG/P 1374, 1375, 1376, 1389, 1390, 1413, Couga Dam, F. L. Farquharson, July 1967; AMG/P 1402, 1412, Wit R, F. L. Farquharson,

July 1967; AMG/P 1415, 1416, Loerie Dam, F. L. Farquharson, July 1967; AMG/P 1562, 1563, Hankey, C. M. Gaigher, October 1970; AMG/P 1741, Wit R, P. H. Skelton, June 1972; AMG/P 1742, 1803, Bukkraal R, P. H. Skelton, June 1972; AMG/P 1751, Kleinberg R, H. Hofmeyer, November 1964; AMG/P 1921, Wit R, P. H. Skelton, April 1973; AMG/P 2533, Hankey, B. Donnelly, August 1966; AMG/P 3789, Hankey, D. Heard, October 1976; AMG/P 3792, Diepkloof R, D. Heard, October 1976; AMG/P 5841, Wit R, J. Hoffman, March 1977; AMG/P 7465, Wit R.

f—Kabeljous River: SAM 19321, C. W. Thorne, November 1938; AMG/P 3805, Kranzplaas, D. Heard, October 1976; AMG/P 3807, Misgund, D. Heard, October 1976.

g—Seekoei River: SAM 19323, C. W. Thorne, November 1938.

h—Kromme River: SAM 19325, Geelhoutboom R, C. W. Thorne, November 1938; SAM 19326, C. W. Thorne, November 1938; AMG/P 230, Assegaaibos, R. A. Jubb, February 1958; AMG/P 1739, Assegaaibos, P. H. Skelton, June 1972; AMG/P 1801, Assegaaibos, P. H. Skelton, September 1972; AMG/P 2082, Assegaaibos, P. H. Skelton, December 1973; AMG/P 2651, Assegaaibos, P. H. Skelton, January 1975; AMG/P 3103, Assegaaibos, ex aquarium, August 1975; AMG/P 3460, Assegaaibos, P. H. Skelton, October 1975; AMG/P 3810, Assegaaibos, D. Heard, October 1976; AMG/P 3811, Melkhoutkraal, D. Heard, October 1976; AMG/P 3812, Witels R, D. Heard, October 1976; AMG/P 3813, Damsekloof, D. Heard, October 1976; AMG/P 3815, Eerstedrif R, D. Heard, October 1976; RUSI 304, Holotype, *Barbus senticeps*, Assegaaibos, J. L. B. Smith.

i—Tsitsikamma River: AMG/P 3568, Sarnia, P. H. Skelton, October 1975; AMG/P 3816, 3817, Palmiet R, D. Heard, October 1976.

j—Bloukrans River system: AMG/P 1707, 1742, P. H. Skelton, April 1972; AMG/P 2652, P. H. Skelton, January 1975; AMG/P 2654, Vark R, P. H. Skelton, January 1975; RUSI 75–120, J. L. B. Smith, March 1965.

k—Groot River: AMG/P 1706, P. H. Skelton, April 1972; AMG/P 2656, P. H. Skelton, January 1975; AMG/P 3456, P. H. Skelton, October 1975.

l—Keurbooms River system: SAM 19334, Edmonton, C. W. Thorne, November 1938; SAM 19335, Paardekop, C. W. Thorne, November 1938; SAM 19337, C. W. Thorne, November 1938; SAM 22333, no data; AMG/P 1784, Diep R, P. H. Skelton, September 1972; AMG/P 1789, De Vlug, P. H. Skelton, September 1972; AMG/P 3461, Diep R, P. H. Skelton, October 1975; AMG/P 3823, Diep R, D. Heard, October 1976; AMG/P 3826, Boegoeskraal, D. Heard, October 1976.

m—Knysna River system: AMG/P 113, Gouna R, R. A. Jubb; AMG/P 152, R. A. Jubb, February 1958; AMG/P 1790, Grootkop R, P. H. Skelton, September 1972.

n—Goukamma river: SAM 19338, Homtini R, C. W. Thorne, November 1938; AMG/P 100, Homtini R, R. A. Jubb, November 1957; AMG/P 110, Homtini R, R. A. Jubb; AMG/P 584, Homtini R, R. A. Jubb, 1958.

o—Karatara River: SAM 19196, Ruigtevlei, C. W. Thorne, October 1938; SAM 19343, Ruigtevlei, C. W. Thorne, November 1938; AMG/P 1793, P. H. Skelton, October 1972.

p—Klein Brak River: SAM 19345, Haalkraal, C. W. Thorne, November 1938.

Notes on the taxonomy

The identity of *B. afer* remained obscure until Jubb (1965) re-examined the three syntypes of the species from the Berlin Museum. The original locality of the species was given by Peters

(1864) as "Cape of Good Hope". The specimens were collected by Ludwig Krebs during the 1820's when he spent some time in the Port Elizabeth–Uitenhage area (ffolliott and Liversidge, 1971). Dr R. Liversidge discussed the probable original collecting locality with Dr R. A. Jubb (Jubb, pers. comm.) and on the available evidence they concluded that the likely locality was the Swartkops River system (Jubb, 1965).

Diagnosis

A fusiform redfin minnow with a single pair of (usually) long barbels and moderately large scales. The intestine is involuted and extends to 2,3 times the SL in adult specimens. The pigmentation frequently includes a mid-lateral band on the body and a bi-lateral series of predorsal spots. *Pseudobarbus afer* is most similar to *P. asper* from which it differs in having larger scales, a relatively shorter intestine and in details of pigmentation. It is also superficially similar to *P. tenuis* from which it may be distinguished by its deeper body proportions and differences in pigmentation (*P. afer* usually does not have a dark mid-predorsal stripe characteristic of *P. tenuis*). Internally these two species differ in pharyngeal teeth and length of the intestine.

Description

The morphometric and meristic data for *P. afer* are given in Table 18. The species attains 110 mm SL. The length of the head is sub-equal to the depth of the body. The eyes are moderately large and lateral in position. The mouth is sub-terminal, sickle-shaped and protrusible. The lips are moderately fleshy. The barbels attached from behind the rictus of the mouth are usually longer than the orbit diameter in adult specimens. There is, however, considerable interspecific variation between populations in barbel length with longest barbels being recorded from the Tsitsikamma-Knysna area. The body is deepest around the origin of the dorsal and pelvic fins. The caudal peduncle is twice as long as deep. The cycloid scales are radiately striated in all fields from a centralized focus, with a mode of 12 striae. Scales on the chest are reduced and embedded and there are no distinctive triangular pelvic axillary scales.

TABLE 18.

Morphometric and meristic measurements of *P. afer* (N=287)

Measurement	*Range*		
	Max.	Min.	$\overline{M}$
Standard length (mm)	104,0	43,0	
Head length (%SL)	30,4	25,4	27,9
Head depth (%HL)	79,4	62,1	71,5
Snout length (%HL)	41,8	29,7	34,9
Orbit diameter (%HL)	32,9	18,7	26,5
Postorbit length (%HL)	51,2	42,2	45,9
Interorbit length (%HL)	39,2	24,5	29,8
Predorsal length (%SL)	55,7	48,7	52,0
Postdorsal length (%SL)	50,9	44,3	48,0
Dorsal fin base (%SL)	15,8	11,0	13,4

Measurement		Range Max.	Min.	$\overline{M}$
Dorsal fin length (%SL)		26,9	17,6	23,4
Pectoral fin length (%SL)		26,1	16,1	18,5
Pelvic fin length (%SL)		20,4	14,2	17,4
Anal fin length (%SL)		23,5	16,6	20,8
Anal fin base (%SL)		12,2	9,0	20,8
Body depth (%SL)		30,6	22,5	26,3
Body width (%SL)		20,5	11,5	17,1
Caudal peduncle length (%SL)		27,6	21,3	24,6
Caudal peduncle depth (%SL)		14,7	10,3	12,4
Anterior barbel length (%OD)				
Posterior barbel length (%OD)		169,6	37,0	94,4
Pectoral–pelvic length (%SL)		28,2	19,5	24,2
Pelvic–anal length (%SL)		18,4	12,4	14,9
Pharyngeal bones L/W	(N = 212)	4,3	2,7	3,5
Length of intestine	(N = 180)	225,0	68,0	146,7

Meristics	
Dorsal fin rays	iii–iv (iv) + 6–8 (7)
Anal fin rays	iii–iv (iii) + 5–6 (5)
Pectoral fin rays	13–17 (15)
Pelvic fin rays	7–9 (8)
Total Vertebrae	35–39 (36–37)
Precaudal vertebrae	17–20 (18–19)
Caudal vertebrae	16–20 (18–19)
Predorsal vertebrae	11–13 (12)
Preanal vertebrae	18–21 (19–20)
Lateral line scales	25–38 (32–37)
Caudal peduncle scale rows	10–18 (16)
Scale rows lat. line–dorsal	4–7 (5–6)
Scale rows lat. line–pelvic	3–6 (4)
Scale rows lat. line–anal	3–5 (4–5)
Predorsal scale rows	13–22 (15–16)
Primary scale radii ($\overline{M}$ to nearest whole no.)	12
Pharyngeal teeth (mode)	2, 3, 5,–5, 3, 2

The paired fins are sexually dimorphic, being longer and more expansive in males in which the pectorals may reach or extend beyond the base of the pelvics and the pelvics reach the base of the anal. The posterior edge of the dorsal and anal fins is straight or mildly convex. The dorsal fin originates just behind the anterior margins of the pelvic fin bases. The caudal is forked with blunt or rounded lobes.

There are 2–3 + 6–8 short blunt gill rakers on the leading edge of the anterior gill arch. The pharyngeal bones are falcate with a length/width ratio of 2,7–4,2. The pharyngeal tooth formula is usually 2, 3, 5–5, 3, 2 but in certain populations (e.g. the Groot River at Natures Valley) 1, 3, 5–5, 3, 1 predominates. The crowns of the pharyngeal teeth are usually closely applied and

obliquely truncate through wear to form a scraping type of occluding surface. The intestine is involuted up to 2,3 times the SL.

Adult males develop large conical tubercles on the snout and head dorsum. The tubercles are best developed in larger specimens during early and mid-summer when breeding takes place. The pattern of the tubercles on the head includes clusters of three to four tubercles on the snout, linear series of tubercles above the nares and orbits and scattered tubercles on top of the head. Bands of minute tubercles three to four deep occur on the dorsal side of branched pectoral fin rays. All other fins have single rows of minute tubercles over the rays and a single row of minute conical tubercles develop on the free edge of the scales.

In life the colour of *P. afer* depends on the habitat: specimens from deeply stained clear waters of the Tsitsikamma region are a dark brown or black with lighter underparts; specimens from lighter environments are olive-brown above and silvery or off-white below. The operculum and iris of the eye are metallic gold with an infusion of red. The fins are hyaline with bright red proximal halves and brown fin-rays. Pigmentation is variable but there is usually a thin unbroken lateral stripe from behind the head to the base of the caudal fin, as well as a bi-lateral series of small spots in the predorsal region or, less frequently, a single mid-predorsal stripe. These markings manifest themselves more clearly in preserved specimens.

The lateral line runs more-or-less straight along mid-body and is either complete or nearly complete. Of the cephalic lateral line system there is no mandibular canal (vestigial segments have been observed in a few individuals) and the preopercular canal is disjunct from the post-ocular commissure.

Distribution

Pseudobarbus afer has been reported from coastal rivers east of the Gourits River system to the Sundays River system which enters Algoa Bay east of Port Elizabeth (Fig. 37A). Along the Outeniqua–Tsitsikamma coastal plain the species is known from only the deeply entrenched river systems of Tertiary origin. A single relict population only is found in the Sundays River system.

Conservation status

P. afer was included in the South African Red Data Book, Fishes as a rare species by Skelton (1977). The taxonomic adjustment of this species by the present study has greatly increased the geographic range of the species. Although many populations have been eliminated and the species is severely depleted in places, overall it is considered safe and is not included in the revised South African Red Data Book, Fishes (Skelton, 1987). Strict conservation of all populations of the species is necessary.

Etymology

The species name *afer* refers to its presence in "Africa."

Pseudobarbus asper (Boulenger 1911).

Fig. 42.

Synonymy

Barbus burchelli (*non* Smith 1841): Weber 1897, 153 (in part, specimens from the Buffels River, Laingsburg and the Kammanassie River).

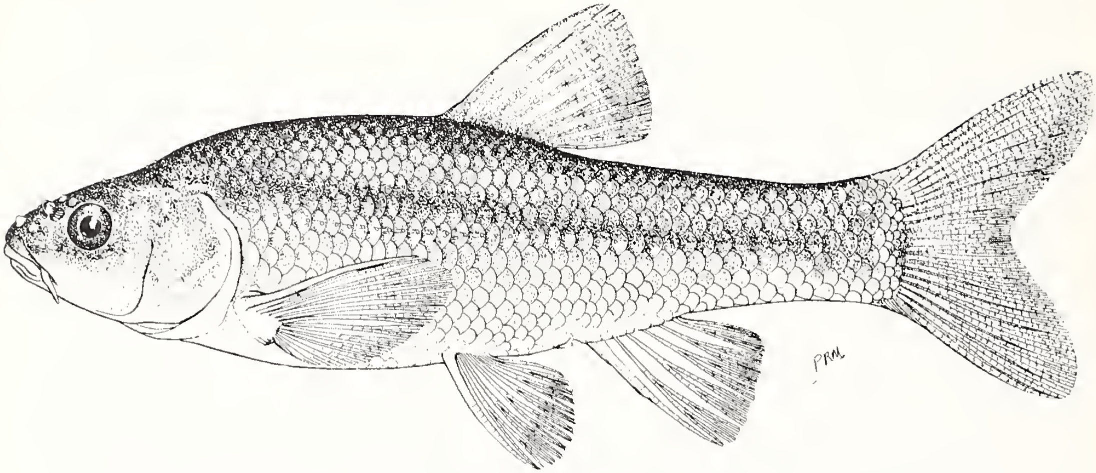

Fig. 42. *Pseudobarbus asper* (Boulenger 1911), AMG/P 9932, male, 63 mm SL, Drawn by P. Meakin.

Barbus asper Boulenger 1911, 176–177, Fig. 154. Type locality: "Cape Colony. Groote R., Sleytlerville. Le Roux R., Ondtsloon." (Sleytlerville = Steytlerville; Ondtsloon = Oudtshoorn). Gilchrist and Thompson 1913, 427–579, Fig. 86; Barnard 1938b, 84; Barnard 1943, 196–200, Fig. 19a (in part, the specimens from locality (a) p. 197, except those from Haalkraal); Jubb 1965, 28–29 (in part, only specimens from the Gourits River system and the Groot River of the Gamtoos River system); Jubb 1967, 99 (in part, only specimens from the Gourits River system and the Groot River of the Gamtoos River system).

Material examined

Holotype: BMNH 1909.12.8.10, male, 73 mm SL, donated by the SAM, collected from Steytlerville on the Groot River, Gamtoos River system.

Paratypes: BMNH 1909.12.8.6–9 , female, 96 mm SL, male 67 mm SL, juvenile 34 mm SL, donated by SAM, collected from the Le Roux River near Oudtshoorn, Gourits River system; SAM 10644, 1 specimen in extremely poor condition, not measured, collected from the Le Roux River near Oudtshoorn, Gourits River system (this specimen is labelled as a "co-type" but is not mentioned by Boulenger 1911 in the original description).

Other material: a—Groot River, Gamtoos River system : SAM 19205, Fullarton, C. W. Thorne, October 1938; SAM 19206, Steytlerville, C. W. Thorne, October 1938; AMG/P 1744, P. H. Skelton, June 1972; AMG/P 1745, Steytlerville, P. H. Skelton, June 1972; AMG/P 3060, Sandfort West, P. H. Skelton, July 1975; AMG/P 3064, Groot River Poort, P. H. Skelton, July 1975; AMG/P 3065, Bucklands, Groot R, P. H. Skelton, July 1975; AMG/P 3066, Weymouth, P. H. Skelton, July 1975; AMG/P 3456, Wit R, 1st drift, P. H. Skelton, October 1975; AMG/P 3458, Wit R, Armansvriend, P. H. Skelton, October 1975.

b—Gourits River system : SAM 10664, Le Roux R; SAM 10673, Grobbelaars R; SAM 14284, Leeus R, S. H. Haughton, 1916; SAM 18945, Grobbelaars R, K. H. Barnard, October 1937; SAM 18957, Langtouw R, K. H. Barnard, October 1937; SAM 18959, Zanddrift, K. H.

Barnard, October 1937; SAM 18952, Meiringspoort, K. H. Barnard, October 1937; SAM 18962, Buffels R, K. H. Barnard, October 1937; SAM 18965, Touws R, K. H. Barnard, October 1937; SAM 18941, Buffels R, K. H. Barnard, October 1937; SAM 19497, Doorn R, K. H. Barnard, April 1939; SAM 18990, Weiders R, K. H. Barnard, February 1938; SAM 18991, Valsch R, K. H. Barnard, February 1938; SAM 18949, Gamka Poort, K. H. Barnard, October 1937; SAM 18956, Moeras R, K. H. Barnard, October 1937; AMG/P 42, Meiringspoort, R. A. Jubb, November 1960; AMG/P 376, Meiringspoort, R. A. Jubb, October 1960; AMG/P 607, Meiringspoort, R. A. Jubb, October 1961; AMG/P 1695 and 1696, Jan Muller Bridge, Touws R, P. H. Skelton, April 1972; AMG/P 1699, VanWyksdorp, P. H. Skelton, April 1972; AMG/P 1703, Gamka R, P. H. Skelton, April 1972; AMG/P 1786, 1787 and 1788, Meiringspoort, P. H. Skelton, September 1972; AMG/P 1943, 1945, Meiringspoort, P. H. Skelton, April 1973; AMG/P 1956, Olifants R, R. E. Stobbs, September 1972; AMG/P 2661, Diep R, P. H. Skelton, January 1975; AMG/P 2663, Rusoord, P. H. Skelton, January 1975; AMG/P 2668, Kruis R, P. H. Skelton, January 1975; AMG/P 4279, Jan Muller Bridge, Touws R, M. Currey, March 1977; AMG/P 4281, VanWyksdorp, M. Currey, March 1977; AMG/P 4289, Meiringspoort, M. Currey, March 1977; AMG/P 6561, Kammanassie R, S. C. Thorne, August 1978; AMG/P 6033, Nels R, S. C. Thorne, August 1978; AMG/P 6045, 6052, Olifants R, S. C. Thorne, August 1978; AMG/P 6055, De Rust, S. C. Thorne, August 1978; AMG/P 6058, 6059, Groot R, S. C. Thorne, August 1978; AMG/P 6062, 6065, 6066, 6068, 6070, 6072, Meiringspoort, S. C. Thorne, August 1978; AMG/P 6078, Kammanassie R, S. C. Thorne, August 1978; AMG/P 6085, Grobbelaars R, S. C. Thorne, August 1978; AMG/P 6099, Olifants R, S. C. Thorne, August 1978; AMG/P 6103, Gourits R, S. C. Thorne, August 1978; AMG/P 6107, 6112, Groot R, S. C. Thorne, August 1978; AMG/P 6115, Touws R, S. C. Thorne, August 1978; AMG/P 6118, Groot R, S. C. Thorne, August 1978; AMG/P 6123, Gamka R, S. C. Thorne, August 1978; AMG/P 6128, Brak R, S. C. Thorne, August 1978; AMG/P 6131, 6133, Jan Muller Bridge, Touws R, S. C. Thorne, August 1978; AMG/P 6136, Weiders R, S. C. Thorne, August 1978; AMG/P 6561, Kammanassie R, S. C. Thorne, August 1978; RUSI 75–139, Kammanassie R.

Diagnosis

A relatively deep-bodied fusiform redfin minnow with a single pair of barbels and small scales (35–45 in the lateral line series). The pharyngeal teeth are obliquely worn and the intestine is relatively long and involuted up to 3,8 times the SL. The pigmentation is distinct with fine melanophores within the scale centres giving a "speckled hen" effect. The small scales and deep body, pharyngeal teeth and longer intestine separate this species from *P. tenuis* with which it is found in the Gourits River system. The small scales, pigmentation and longer intestine distinguishes this species from *P. afer* in the Gamtoos River system.

Description

Morphometric and meristic measurement data for *P. asper* are given in Table 19. The head is subequal to the body depth and the lateral head profile is rounded. The eyes are lateral in position. The mouth is sub-terminal and sickle-shaped with thin to moderately thick lips. The single, simple barbels from the corners of the mouth are shorter than the orbit diameter in adults. The gill openings are broadly attached to the isthmus.

The body is oval in cross-section and the caudal peduncle slightly more than twice as long as deep. The scales are cycloid and radiately striated with a mode of 11 radii in all fields from a central focus. Breast and ventral scales between the pectoral and pelvic fins are reduced in size

TABLE 19.

Morphometric and meristic measurements of *P. asper* (N = 110)

Measurement		*Range* Max.	Min.	$\overline{M}$
Standard length (mm)		80,0	43,0	58,9
Head length (%SL)		28,2	24,7	26,5
Head depth (%HL)		76,4	66,8	71,7
Snout length (%HL)		38,0	31,1	33,9
Orbit diameter (%HL)		28,7	22,0	26,0
Postorbit length (%HL)		52,1	37,8	47,0
Interorbit length (%HL)		35,2	25,5	31,2
Predorsal length (%SL)		54,6	47,8	51,0
Postdorsal length (%SL)		52,2	45,5	49,0
Dorsal fin base (%SL)		15,7	11,3	13,2
Dorsal fin length (%SL)		27,9	18,9	23,0
Pectoral fin length (%SL)		26,1	17,0	21,1
Pelvic fin length (%SL)		21,8	12,6	16,6
Anal fin length (%SL)		24,3	16,8	20,2
Anal fin base (%SL)		13,3	8,5	10,2
Body depth (%SL)		29,5	21,5	26,4
Body width (%SL)		20,0	10,9	16,7
Caudal peduncle length (%SL)		29,6	21,5	25,3
Caudal peduncle depth (%SL)		13,2	9,6	11,6
Anterior barbel length (%OD)		—	—	—
Posterior barbel length (%OD)		116,3	46,0	70,7
Pectoral–pelvic length (%SL)		29,8	21,1	25,1
Pelvic–anal length (%SL)		17,6	11,8	14,6
Pharyngeal bones L/W	(N = 74)	4,0	2,8	3,3
Length of intestine (%SL)	(N = 81)	381,6	124,2	240,0

Meristics	
Dorsal fin rays	iii–iv (iv) + 6–8 (7)
Anal fin rays	iii–iv (iii) + 5–6 (5)
Pectoral fin rays	14–17 (15–16)
Pelvic fin rays	7–9 (8)
Total Vertebrae	35–38 (36)
Precaudal vertebrae	17–20 (19)
Caudal vertebrae	16–19 (17–18)
Predorsal vertebrae	11–13 (12)
Preanal vertebrae	18–21 (19–20)
Lateral line scales	35–45 (37–40)
Caudal peduncle scale rows	16–22 (18–20)
Scale rows lat. line–dorsal	6–9 (7–8)
Scale rows lat. line–pelvic	5–8 (6)

Meristics	
Scale rows lat. line–anal	5–8 (6)
Predorsal scale rows	18–26 (21–22)
Primary scale radii ($\overline{M}$ to nearest whole no.)	11
Pharyngeal teeth (mode)	2, 3, 5–5, 3, 2

and deeply embedded. The nape scales are reduced and crowded. There are no trianguloid or elongated pelvic axillary scales.

In adults the paired fins are sexually dimorphic with males having longer more expansive fins than the females. The pectorals reach the base of the pelvic fins in adult males. The fins of the Gamtoos River specimens are relatively longer than those of specimens from the Gourits system. The pelvics are sub-rectangular reaching the anterior base of the anal fin in adult males. The posterior edge of the dorsal and anal fins is straight or slightly convex. The anterior origin of the dorsal fin is placed behind the origin of the pelvic fins. The caudal fin is forked with narrowly rounded lobes.

There are 2–4 + 7–10 short, stubby gill rakers on the leading arch. The pharyngeal bones are falcate with a length/width ratio of 2,8–4. The pharyngeal teeth are in three rows with a formula of 2, 3, 5–5, 3, 2. The crowns of the pharyngeal teeth are closely applied and obliquely truncated to form an effective scraping type of occlusal surface. The intestine is long and involuted in a series of coils. The peritoneum is black.

Breeding males develop large conical tubercles on the head dorsum and on the snout. The pattern, size and number of these tubercles is similar to *P. afer*. In addition bands of fine tubercles up to three or four deep develop over the branched pectoral fin rays, with single rows of minute tubercles on the rays of other fins and a single row along the posterior free edge of the scales. Large mature and ripe females may develop a few small tubercles on the head dorsum.

The general colour of *P. asper* depends on the habitat but is usually light brownish above with silvery flanks and whitish underparts. There is an uneven dark lateral band from behind the head to the base of the caudal fin. Fine melanophores in the scale centres give an overall "speckled hen" appearance. The opercula are metallic golden and the iris of the eyes silvery-golden. The proximal half of the fins becomes bright scarlet in adults especially in mature and ripe males. Distal fin membranes are hyaline and the rays are a light brown.

The lateral line is generally incomplete and runs more-or-less straight along the mid-body. The cephalic lateral line lacks a mandibular canal and the pre-opercular canal is disjunct from the post-ocular commissure. As with other *Pseudobarbus* species the supraneural bones are vestigial or absent and the anterior epineurals are poorly ossified and reduced.

Distribution

P. asper occurs in the Groot River of the Gamtoos River system as well as in the larger tributaries and mainstream of the Gourits River system (Figs. 35 and 37A). It is often found in standing water bodies and has been collected in large numbers in certain localities.

Conservation status

P. asper was considered a rare species by Skelton (1977). In a recent reassessment of this status the species is now regarded as "safe" and is not included in the revised version of the

South African Red Data Book, Fishes (Skelton, 1987). The reason for this change is that distribution surveys of the Gourits and Gamtoos River systems by the CDNEC show the species to be widespread and relatively common throughout its range. It can survive harsh conditions in temporary pools and does well in impounded waters (Gaigher *et al.*, 1980).

Etymology

The name *asper* refers to the rough tubercles on the head of males.

Pseudobarbus quathlambae (Barnard 1938)

Fig. 43.

Synonymy

Labeo quathlambae Barnard 1938a, 525–528, Fig. p. 52, type locality: "Upper Umkomazana River, at an altitude of about 5300 ft. Himeville"; Jubb 1966a, 161–162; Jubb 1966b, 78–80; Jubb 1967, 115, Fig. 117 a, b.

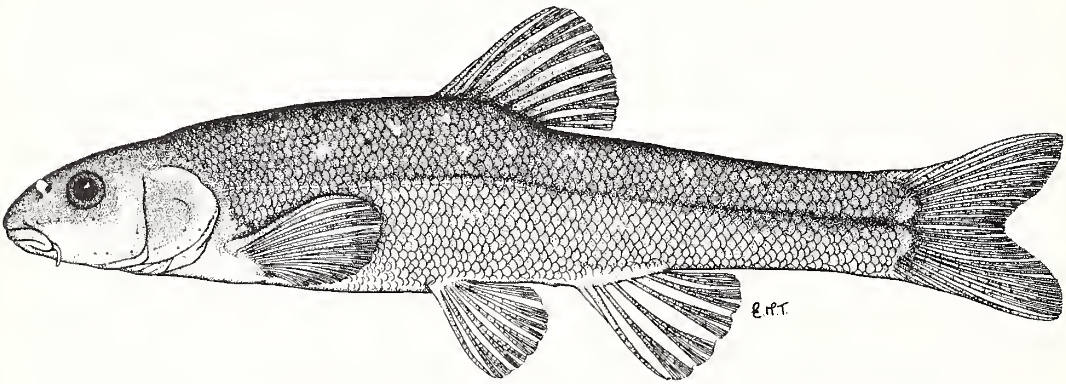

Fig. 43. *Pseudobarbus quathlambae* (Barnard 1938), AMG/P 3473, male, 95 mm SL. Drawn by E. Tarr.

Oreodaimon quathlambae, Greenwood and Jubb 1967, 17–37, 17 figures; Jubb 1971, 4–7; Pike and Tedder 1973, 9–15; Skelton 1974 a, 215–222; Skelton 1976, 407–408, Fig 10a; Rondorf 1976, 150–151; Gephard 1978, 105–111.

Material examined

Lectotype: SAM 19018, female, 80 mm SL, Upper Umkomazana River near Himeville, Natal, R. S. P. Vaughan, 1937.

Paralectotypes: SAM 19018, 14 specimens 28–71 mm SL, collected from the Upper Umkomazana River near Himeville, Natal, by A. M. Copland, August 1937; NMP 1416, 33 specimens 30–37.8 mm SL, collected with the other paralectotypes.

Other material: all Orange River system in Lesotho: AMG/P 1540 and 3477, Tsoelikana R, A. Tedder, November 1970; AMG/P 1877, 3476, 3478, Tsoelikana R, A. Tedder, April 1972;

AMG/P 1823, 1824, Tsoelikana R, P. H. Skelton, January 1973; AMG/P 3473, Tsoelikana R, P. H. Skelton, October 1975; AMG/P 3474, Tsoelikana River, D. Rondorf, Nov 1974; AMG/P 3475, Tsoelikana R, D. Rondorf, January 1975; AMG/P 3479, Moremoholo R, D. Rondorf, July 1975; AMG/P 3480, Senqu R, D. Rondorf, August 1975; RUSI 25491, Jordane R, tributary of the Senqunyane R, K. J. Meyer, 27 October 1985.

Notes on the taxonomy

Barnard (1938a) described this species from 58 specimens of which the author has been able to locate the above 48 in the SAM and NMP collections. As clearly stated by the then editor of the Annals of the Natal Museum, Mr R. J. P. Vaughan collected the first specimen, which is the largest in the type series. This specimen was designated the lectotype by Greenwood and Jubb (1967). Barnard (1938a) stated that a second specimen was obtained from the same locality as the lectotype but this specimen cannot be differentiated from other paralectotypes because its dimensions were not specified in the original description.

In regard to the type locality, Crass (1977 and 1985) believes that the original specimens may have come from Lesotho and not the Umkomazana River. Crass's argument is based on the fact that the species is now known from Lesotho and has not been found since in the Umkomazana River. Furthermore the Sani Pass (Umkomazana River valley) was an important trade route to Natal from Lesotho. Against this argument is the published information by Barnard (1938a) supported by the editor and then Director of the Natal Museum, Dr R. F. Lawrence, that the specimens came from the Upper Umkomazana River near Himeville. In addition there is a letter written by Mr R. S. P. Vaughan to Dr R. A. Jubb in 1966 (RUSI files) in which he states explicitly: "I remember the occasion when I went to the Umkomazana River with J. McVey Brown and Hardingham (both of whom have since died). Copland had nothing to do with catching these minnows. He either took or sent the specimens to P. M. Burg." The author therefore believes that the evidence supports the Umkomazana River as the type locality, and that subsequently the species has been extirpated from that locality. A description of the type locality is given by Greenwood and Jubb (1967) and Jubb (1971).

Diagnosis

This is an unmistakeable species with extremely small scales, a single pair of short barbels, pharyngeal teeth in two rows only and the intestine is relatively short, subequal to the SL. *Pseudobarbus quathlambae* is most similar to *P. tenuis* but cannot be confused with this latter species on account of the large difference in scale size between them.

Description

The morphometric and meristic data are given in Table 20. The species attains 130 mm SL and has a terete body with the length of the head greater than the body depth. The head profile is bluntly rounded or ellipsoid and the mouth is sub-terminal in position. The mouth is sickle-shaped and protrusible and the lips are moderately fleshy and well developed. A single short (less than the orbit diameter) simple barbel occurs on either side at the corner or angle of the mouth. The gill openings are broadly attached to the isthmus.

In cross section the body is oval with the caudal peduncle more than twice as long as deep. The tiny scales are radiately striated with a central focus. The ventral scales from the isthmus to the pelvic fins (breast and belly) are reduced and embedded giving a naked appearance to the

TABLE 20.

Morphometric and meristic measurements of *P. quathlambae* (N=32)

Measurement		*Range* Max.	Min.	$\overline{M}$
Standard length (mm)		102,0	46,0	
Head length (%SL)		27,1	22,7	24,8
Head depth (%HL)		69,4	59,9	64,3
Snout length (%HL)		39,3	33,3	36,8
Orbit diameter (%HL)		27,9	19,4	23,6
Postorbit length (%HL)		57,8	46,4	49,7
Interorbit length (%HL)		30,2	24,4	27,4
Predorsal length (%SL)		55,0	47,4	50,8
Postdorsal length (%SL)		52,6	45,0	49,3
Dorsal fin base (%SL)		13,5	10,5	11,9
Dorsal fin length (%SL)		22,0	17,7	19,8
Pectoral fin length (%SL)		21,7	15,5	18,8
Pelvic fin length (%SL)		16,7	12,8	15,1
Anal fin length (%SL)		20,0	15,1	17,5
Anal fin base (%SL)		12,1	8,9	10,2
Body depth (%SL)		25,5	20,0	22,0
Body width (%SL)		16,7	11,9	14,7
Caudal peduncle length (%SL)		28,2	22,8	25,3
Caudal peduncle depth (%SL)		12,1	9,9	11,0
Anterior barbel length (%OD)		—	—	—
Posterior barbel length (%OD)		80,7	34,2	56,3
Pectoral–pelvic length (%SL)		27,7	23,0	25,5
Pelvic–anal length (%SL)		17,5	12,7	14,9
Pharyngeal bones L/W	(N = 28)	4,3	2,7	3,2
Length of intestine (%SL)	(N = 20)	114,3	77,4	96,2

Meristics	
Dorsal fin rays	iii + 6–8 (7)
Anal fin rays	iii + 5–6 (5)
Pectoral fin rays	15–17 (16)
Pelvic fin rays	7–9 (8)
Total vertebrae	38–40 (39)
Precaudal vertebrae	19–22 (20–21)
Caudal vertebrae	17–20 (18–19)
Predorsal vertebrae	13–15 (14)
Preanal vertebrae	20–22 (21)
Lateral line scales	60–72 (65–67)
Caudal peduncle scale rows	30–38 (32–36)
Scale rows lat. line–dorsal	10–14 (11–12)
Scale rows lat. line–pelvic	8–12 (10–11)

Meristics	
Scale rows lat. line–anal	9–11 (9–10)
Predorsal scale rows	28–40 (34–36)
Primary scale radii ($\overline{M}$ to nearest whole no.)	10
Pharyngeal teeth (mode)	3, 4–4, 3

region. The nape scales are also reduced and there are no elongated or trianguloid pelvic axillary scales. The scales adjacent to the dorsal and anal fin bases are reduced and embedded.

The paired fins of mature males are longer and more rounded than those of the females. In both sexes the pectoral fins do not reach the bases of the pelvic fins and the pelvics do not reach the base of the anal fin. All fins have rounded convex edges and the caudal fin is shallow forked with rounded lobes. The dorsal fin originates behind the anterior base of the pelvic fins.

There are 1–2 + 5–7 short blunt gill rakers on the outer leading edge of the anterior arch. The pharyngeal bones are falcate with a length to width ratio of 2,8–4,3. The pharyngeal teeth are in two rows 3, 4–4, 3. The pharyngeal teeth are semi-cylindrical with deflexed crowns with off-centre recurved conical tips. The intestine is short (sub-equal to the SL) and has a single "S"-flexure.

Sexually mature and ripe adults of both sexes develop small conical tubercles over the dorsal and dorso-lateral parts of the head. There are bands of minute compressed conical tubercles up to six rows across over the branched pectoral fin rays. Single tubercle rows occur over the rays of other fins. There are usually only one or two small conical tubercles on each scale.

Colour depends on the habitat and the physiological state of the individual. Adults vary from a light olive-brown to deep bluish black above and whitish-cream below. The iris is light golden and the operculum metallic gold. Fins are hyaline with light grey or brown rays and the basal membranes and adjacent body regions are bright red. There is usually a dark mid-lateral band from behind the head to the base of the caudal fin. A bi-lateral predorsal series of dark spots or vermiculations form prominent markings on live and preserved specimens from certain populations (see Gephard, 1978).

The lateral line is complete and runs straight mid-laterally along the body. There is no mandibular canal and the pre-opercular canal is reduced anteriorly and disjunct from the post-ocular commissure.

Supraneural bones are vestigial or absent. Anterior epineurals are not ossified and the bones of the anterior portion of the neurocranium are membranous and weakly ossified. Supraorbitals are vestigial and there are usually only four infraorbital bones on either side including the lachrymal.

Distribution

Since its discovery in 1938 the species has not been collected in the type locality (the Umkomazana River) and it is presumed to be extinct there. Populations have been discovered in five tributaries of the Orange or Senqu River in Lesotho (Fig. 37b).

Conservation status

P. quathlambae is an endangered species (Skelton, 1977 and 1987). It is believed to have

been eliminated from the type locality in Natal. In Lesotho the few known populations are limited to relatively short stretches of small streams. In general, stream habitats in the Maluti and Drakensberg Mountains are deteriorating through siltation from overgrazing and poor agricultural practices. Increased environmental pressures on these habitats may result from large-scale development projects such as the Lesotho Highlands Water Scheme.

Etymology

The name *quathlambae* is derived from an indigenous African name for the Drakensberg mountains and means "a barrier of spears".

Barbus **Cuvier and Cloquet 1816**

Type species: *Cyprinus barbus* Linnaeus 1758, by tautonymy.

The genus *Barbus* is generally accepted to be an unnatural and extremely large assemblage of cyprinid species. As many as 292 African species alone were listed by Leveque and Daget (1984). Therefore no attempt is made here to provide a comprehensive definition for this genus (see Howes (1987) for further comments on this problem). Instead certain group characteristics of the two serrated-rayed redfin species and other southern African *Barbus* species are provided for comparison with the genus *Pseudobarbus*.

Some characteristic features of African *Barbus* species are: generally fusiform and slightly compressed bodies; head naked with mouth protrusible and either supra-terminal, terminal or sub-terminal in position; usually one or two pairs of simple barbels but these are absent in some species; lips variable in development frequently showing large intraspecific variation; scales cover entire body , mostly moderate or large in size, cycloid with radiating , convergent or parallel striae in all scale fields; dorsal fin with the last unbranched ray either simple segmented and flexible , simple bony and spinous or bony spinous (with segmented flexible tip) and serrated; anal fin with ii–iv simple and five (occasionally six or seven) branched rays; intestine short with a simple flexure (approximately equal in length to the SL) or moderately elongated and involuted (up to four or five times the SL); pharyngeal bones falcate with three rows of teeth, usually in the formula 2, 3, 5–5, 3, 2; pharyngeal teeth most often hooked or spoon-shaped but also molariform in certain larger species (e.g. Banister 1973).

Characteristic but not necessarily diagnostic features of the two known serrated-rayed redfin species are: anal fin with six or seven branched rays; dorsal fin with last unbranched ray bony and serrated with flexible tip, or segmented and flexible with vestigial serrations; mouth terminal with two pairs of long barbels; pharyngeal bones falcate with hooked or pointed teeth and in three rows with the formula 2, 3, 4 or 5–5 or 4, 3, 2; intestine short (about equal to the SL) in a single flexure; ripe adults of both sexes with scattered minute erupted tubercles (pimples) on the snout and head dorsum, the scales and, in single rows over rays of all fins; cephalic lateral line system with complete preopercular-mandibular canal that is linked to the post-ocular commissure by means of a canal through the antero-dorsal corner of the opercles. Adult fish have bright red patches on the proximal half of fins and adjacent body area. Gill-rakers short, six to nine on the lower limb (ceratobranchial) of the leading gill arch. Total vertebrae 36–39; from five to nine well developed supraneural bones present; frontals overlapping lamellae of supraethmoid; intercalars disc-like and well developed; exoccipitals without posterior flange; supraorbitals slender not in recess in frontals; lachrymal with pointed

or angulate dorsal edge; premaxillae slender; urohyal slender with truncate posterior edge. Paired fins not markedly dimorphic. Intramuscular bones well developed from behind the head.

Barbus calidus Barnard 1938.

Fig. 44.

Synonymy

Barbus serra (*non* Peters 1864): Gilchrist and Thompson 1913, 404 (in part—the 2 smaller Leipoldt specimens).

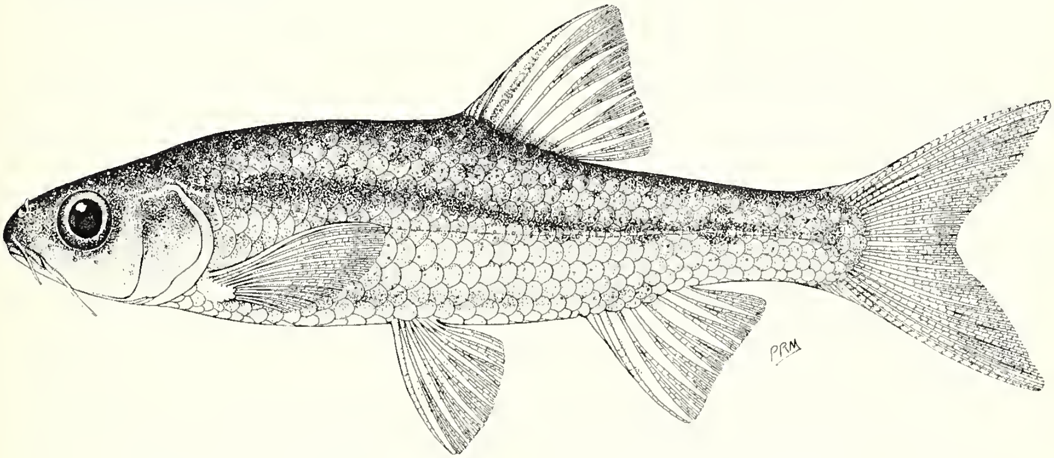

Fig. 44. *Barbus calidus* Barnard 1938, AMG/P 8216, male, 65 mm SL. Drawn by P. Meakin.

Barbus calidus Barnard 1938b, 86. Type locality: "Olifants River system, Clanwilliam, Cape"; Barnard 1943, 176–179, Fig. 15 a–c; Jubb 1965, 25, Fig. 7; Jubb 1967, 95, Fig. 80.

Material examined

Lectotype (new designation): SAM 18605, male, 71 mm SL. Collected by K. H. Barnard and C. W. Thorne, 1936, from the Jan Diessels River, Olifants River system, western Cape Province.

Paralectotypes: SAM 18605, 67, 2–74,6 mm SL, collected with the lectotype; SAM 18606, Tra-Tra River, K. H. Barnard, 1936 (SAM 18605 and SAM 18606 are combined together in one container and the source of individual specimens cannot be determined); SAM 18756, Olifants River, K. H. Barnard, 11 April 1937; the remaining samples of possible paralectotypes have not been seen or traced and are presumed lost—SAM 22499, Boontjies River, K. H. Barnard, November 1936; SAM 215/216, Olifants River, C. L. Leipoldt, 30 November 1897; SAM 2012–2015, Olifants River, Clanwilliam, R. M. Lightfoot.

Other material (all Olifants River system): SAM 19002, Olifants R, K. H. Barnard, 16–18 April 1938; SAM 22478, K. H. Barnard, April 1949; AMG/P 728, Thee R, K. van Rensburg, February 1964; AMG/P 885, K. van Rensburg, 1965; AMG/P 1371, Rondegat R, F. L. Farquharson, April 1967; AMG/P 1393, Keerom, K. van Rensburg, January 1964; AMG/P

1581, Tra-Tra R, R. Louw, November 1968; AMG/P 1644, Noordhoeks R, F. L. Farquharson, April 1967; AMG/P 1797, Rondegat R, P. H. Skelton, September 1972; AMG/P 1818, Thee R, D. Heard, September 1972; AMG/P 1844, Tra-Tra R, P. H. Skelton, January 1973; AMG/P 1850, Jan Diessels R, P. H. Skelton, January 1973; AMG/P 1855, Matjies R, P. H. Skelton, January 1973; AMG/P 1857, Breekkrans R, P. H. Skelton, January 1973; AMG/P 1862, Noordhoeks R, P. H. Skelton, February 1973; AMG/P 1869, Thee R, P. H. Skelton, February 1973; AMG/P 1871, Ratels R, P. H. Skelton, February 1973; AMG/P 1883, Rondegat R, D. Heard, November 1972; AMG/P 2050, Matjies R, P. H. Skelton, October 1973; AMG/P 2051, Noordhoeks R, P. H. Skelton, October 1973; AMG/P 2052, Tra-Tra R, P. H. Skelton, October 1973.

Notes on the taxonomy

Barnard (1938b) did not specifically mention the material he used to describe this species. The lectotype and paralectotypes are taken from all the samples available to Barnard prior to the publication in which it was described. All this material was mentioned in Barnard (1943) but certain samples have not been traced (SAM 215/216/2912/2913/2914/2915 and SAM 22499).

Diagnosis

This is the only redfin minnow with a stout serrated unbranched ray in the dorsal fin and usually six branched rays in the anal fin. The posterior position of the dorsal fin, slender caudal peduncle, terminal mouth with two pairs of barbels, and large eye also distinguish it from other redfin species. It is closest to *B. erubescens* from which it differs in the form of the dorsal fin unbranched ray, the number of anal fin branched rays, the number of predorsal vertebrae, the number and shape of the pharyngeal teeth, and in colour and pigmentation. The number of anal fin branched rays also serves to separate the species from juveniles of the larger *Barbus* species in the Olifants River system (*B. capensis* and *B. serra*).

Description

Morphometric and meristic data are given in Table 21. *B. calidus* is a fusiform minnow species which attains at least 82 mm SL. The length of the head is greater than the body depth. The relatively large mouth is terminal and U-shaped, the lips are thin. There are two pairs of well-developed simple barbels that in adults are equal or greater than the orbit diameter. The relatively large eyes are lateral in position. The branchiostegal membrane is narrowly attached to the isthmus.

The body is completely covered with radiately striated cycloid scales. The radii extend from an anteriorly placed focus in all the scale fields. Chest scales are slightly reduced in size but are distinct and not embedded. A small triangular pelvic axillary scale is present.

The dorsal fin originates behind the pelvic origin and has a straight posterior margin. The last (fourth) unbranched ray is bony and serrated along the posterior edge. The anal fin has three unbranched and six branched rays and the posterior margin is straight. The caudal fin is forked with slender lobes. The pectoral fins are sub-falcate and slender nearly reaching the anterior base of the pelvics. The pelvics are well-developed and triangular in shape. There is no marked sexual dimorphism in the paired fins.

Table 21.

Morphometric and meristic measurements of *B. calidus* (N=280)

Measurement		*Range* Max.	Min.	$\overline{M}$
Standard length (mm)		82,0	22,1	51,5
Head length (%SL)		30,0	24,6	27,5
Head depth (%HL)		76,7	60,9	68,2
Snout length (%HL)		40,0	28,1	34,4
Orbit diameter (%HL)		36,4	25,0	29,1
Postorbit length (%HL)		53,3	38,2	43,6
Interorbit length (%HL)		41,7	28,6	34,1
Predorsal length (%SL)		57,5	50,0	54,3
Postdorsal length (%SL)		50,0	42,6	45,7
Dorsal fin base (%SL)		17,0	12,1	13,8
Dorsal fin length (%SL)		26,0	18,4	22,2
Pectoral fin length (%SL)		23,4	18,6	21,2
Pelvic fin length (%SL)		20,2	16,0	18,2
Anal fin length (%SL)		23,3	17,8	19,6
Anal fin base (%SL)		13,9	9,1	13,4
Body depth (%SL)		27,0	19,4	22,7
Body width (%SL)		18,5	11,9	14,2
Caudal peduncle length (%SL)		25,0	17,4	19,5
Caudal peduncle depth (%SL)		11,6	8,5	10,0
Anterior barbel length (%OD)		133,3	8,7	75,8
Posterior barbel length (%OD)		157,1	41,7	107,8
Pectoral–pelvic length (%SL)		27,2	18,8	23,3
Pelvic–anal length (%SL)		24,1	15,0	18,7
Pharyngeal bones L/W	(N = 18)	5,5	4,0	4,6
Length of intestine (%SL)	(N = 72)	124,3	43,3	89,1

Meristics	
Dorsal fin rays	iii–iv (iv) + 6–8 (7)
Anal fin rays	iii–iv (iii) + 5–7 (6)
Pectoral fin rays	11–15 (13–14)
Pelvic fin rays	7–9 (8)
Total vertebrae	36–39 (37–38)
Precaudal vertebrae	17–20 (19)
Caudal vertebrae	17–20 (18–19)
Predorsal vertebrae	12–14 (13)
Preanal vertebrae	20–22 (21)
Supraneurals	5–9 (7)
Lateral line scales	34–39 (37)
Caudal peduncle scale rows	12–17 (14–16)
Scale rows lat. line–dorsal	5–7 (6)

Meristics

Scale rows lat. line–pelvic	3–4 (3)
Scale rows lat. line–anal	3–5 (4)
Predorsal scale rows	14–21 (17–18)
Primary scale radii ($\overline{M}$ to nearest whole no.)	9
Pharyngeal teeth (mode)	2, 3, 5–5, 3, 2

Breeding adults of both sexes (but especially the males) have numerous small, white, pimple-like excrescent tubercles scattered over the dorsal surface of the head and predorsal scales. Single rows of similar excrescent tubercles overlie the rays of the paired fins.

In life the colour is pale olive green or brownish-yellow with cream or off-white ventral parts. The iris is silvery-gold and the opercula metallic silvery-gold. The fin rays are dark and the fin membranes hyaline distally with scarlet basal portions (usually the caudal fin has only a salmon tinge). A broad dark band passes mid-laterally from behind the head to the posterior end of the caudal peduncle. Irregular dark blotches are scattered over the dorsal body surface. A short strip of dark pigment occurs along the body adjacent to the base of the anal fin. In breeding dress the males are more intensely pigmented and the dark lateral band is prominent.

The lateral line is usually complete and passes more-or-less straight mid-laterally from the head to the base of the caudal fin. The cephalic lateral line system includes a typically complete cyprinid pattern without disjunctions. The pre-opercular canal passes through a supra-preopercular tube on the opercle bone to join the post-ocular commissure.

Distribution

B. calidus is endemic to the Clanwilliam Olifants River system and is restricted to upper reaches of tributaries within the Cape Fold Mountain ranges (Fig. 44). The species is no longer found in the mainstream of the Olifants River itself although certain early records were taken there.

Notes on breeding biology

The author has observed the spawning activity of this species on two occasions. On January 6, 1981 a school of predominantly (at least 90%) male *B. calidus* were seen swimming over a vertical rock face about one meter below the water surface in a large, deep pool (40–50 m long by 10–20 m wide and three to four m deep) of the Ratels River. The specimens were all ripe and running adults and one female caught with the males was partly spent. The second sighting was a similar school of milling male specimens also against a vertical rock face in a small pool of the Rondegat River. Of 27 specimens collected from this school 25 were ripe running males, one was a ripe female, and one was an active but not fully ripe male. All the ripe running specimens collected had well developed tubercles.

Conservation status

The Clanwilliam redfin is a rare fish species (Skelton, 1977 and 1987). The known populations of this species are all isolated and restricted to short stretches of tributaries beyond the reach of smallmouth and largemouth black bass (*Micropterus dolomieu* and *M. salmoides*), introduced predators.

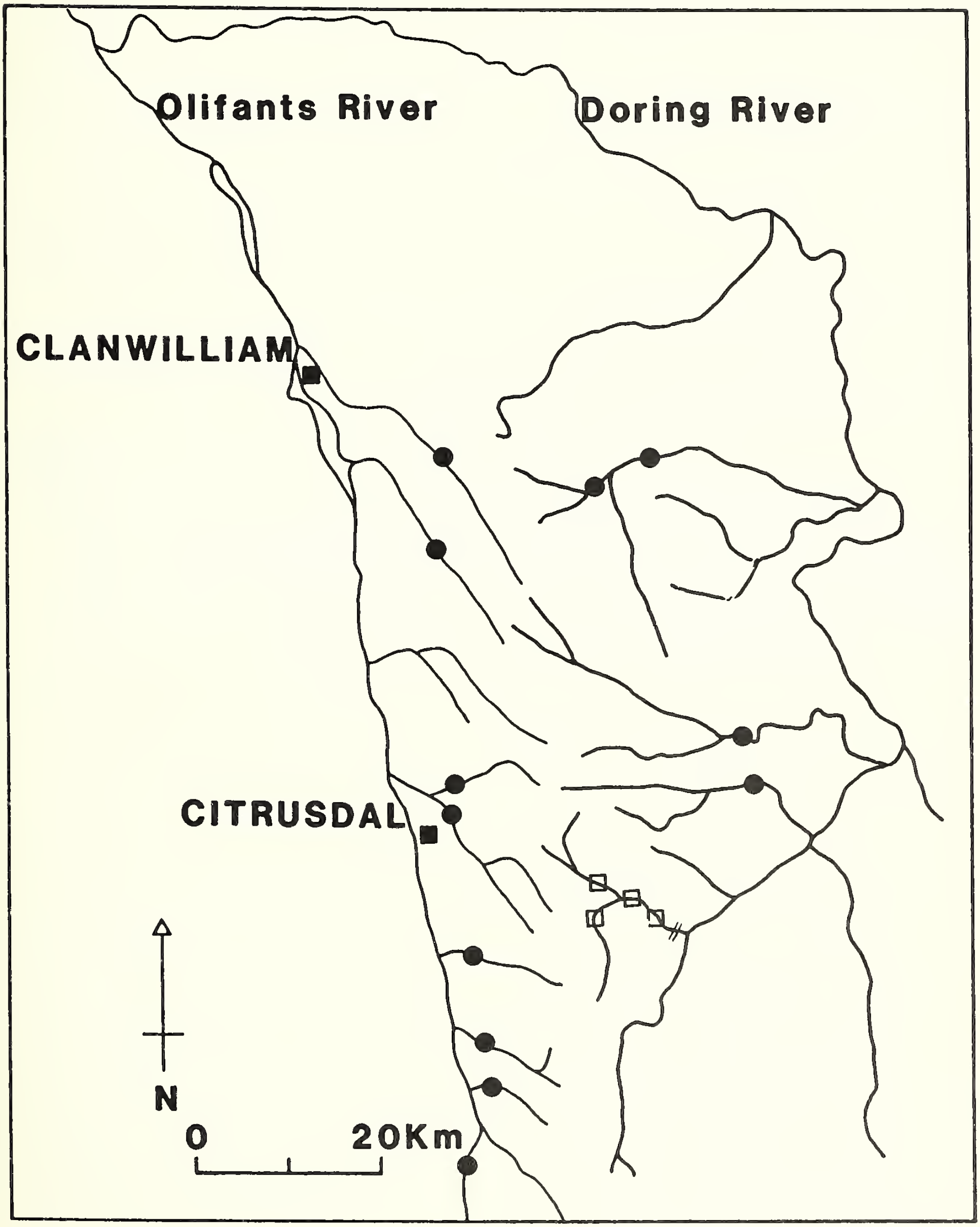

Fig. 45. Distribution of *Barbus calidus* (shaded circles) and *B. erubescens* (unshaded square) in the Olifants River system, based on museum records referred to in this study. Symbols may refer to multiple collection records.

Etymology

The name *calidus*, derived from the latin calidum, meaning hot or a hot drink, refers to the "brightness of the red patches, and the heat of the Olifants River valley in summer time" (Barnard, 1943: 179).

Barbus erubescens Skelton 1974.

Fig. 46.

Synonymy

Barbus calidus (non Barnard): Jubb 1967, 95–97 (in part, the specimens from the population stated as having been discovered by K. J. van Rensburg).

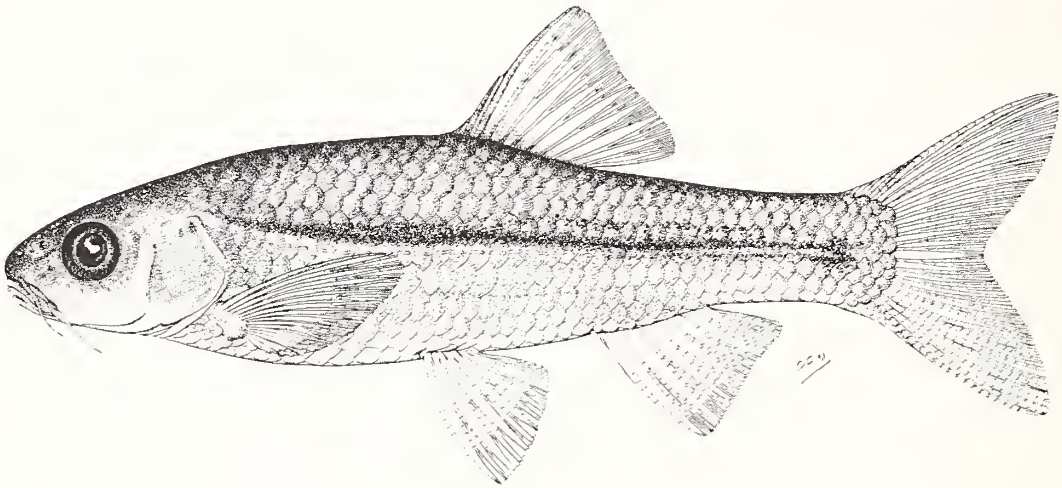

Fig. 46. *Barbus erubescens* Skelton 1974, AMG/P 2043, male, 66 mm SL. Drawn by P. Meakin.

Barbus erubescens Skelton 1974 b, 1–12, Figs 1, 2, 3. Type locality: "Suurvlei River, Olifants River system, western Cape Province, South Africa, 32° 38′ 56″ S., 19° 12′ 21″ E.

Material examined

Holotype: AMG/P 2424, male, 84 mm SL, Suurvlei River, Olifants River system, P. H. Skelton and A. Coetzer, 8 December 1973.

Paratypes: 39 males collected with the holotype: AMG/P 2425 (21); RUSI 74–268 (6); BMNH 1974.6.13, 1–6 (6); MRAC 192175–192180 (6);

5 juveniles, Twee River, P. H. Skelton, 10 October 1973; AMG/P 2426 (2); RUSI 74–266; BMNH 1974.6.13 :9 (1); MRAC 192171 (1).

5 juveniles, Twee River, P. H. Skelton, 6 October 1973: AMG/P 2427 (2); RUSI 74–265; BMNH 1974.6.13:10 (1); MRAC 192172 (1).

5 females, Twee River, P. H. Skelton, 11 October 1973: AMG/P 2428 (2); RUSI 74–267 (1); BMNH 1974.6.13:8 (1); MRAC 192173 (1).

5 females, Middeldeur River, P. H. Skelton and A. Coetzer, 8 December 1973: AMG/P 2429 (2); RUSI 74–269 (1); BMNH 1974.6.13:7 (1); MRAC 192174 (1).

Other material: (all Olifants River system): AMG/P 1388, Twee R, F. L. Farquharson, April 1967; AMG/P 1799, Middeldeur R, P. H. Skelton, September 1972; AMG/P 1866, Middeldeur R, P. H. Skelton, February 1973; AMG/P 1867, Twee R, P. H. Skelton, February 1973; AMG/P 1881, Middeldeur R, D. Heard, November 1972; AMG/P 1882, Middeldeur R, K. J. van Rensburg, March 1964; AMG/P 2043–2049 and AMG/P 3710, Twee R, P. H. Skelton, October 1973; AMG/P 7348, Middeldeur R, I. G. Gaigher, November 1977; AMG/P 7442, Twee R, P. H. Skelton, October 1973.

Diagnosis

B. erubescens differs from all other *Barbus* species in having seven branched rays in the anal fin. It is closest to *B. calidus* from which it differs in the form of the last unbranched dorsal fin ray (flexible and weakly serrated *vs* bony and strongly serrated), the modal number of branched dorsal fin rays (eight *vs* seven) the modal number of predorsal vertebrae (12 *vs* 13), the number and shape of the pharyngeal teeth (2, 3, 4–4, 3, 2 *vs* 2, 3, 5–5, 3, 2), and in the pigmentation and the breeding colouration of males and females.

Description

Morphometrics and meristics are given in Table 22. *B. erubescens* is a fusiform minnow which reaches at least 95 mm SL. The head is longer than the body depth. The mouth is slightly sub-terminal in position, U-shaped and protrusible. The lips are thin and there are two pairs of well-developed barbels that are longer than the orbit diameter in adult fishes. The eyes are lateral to dorso-lateral in position.

TABLE 22.

Morphometric and meristic measurements of *B. erubescens* (N=110)

Measurement	*Range*		
	Max.	Min.	$\overline{M}$
Standard length (mm)	95,0	30,5	64,6
Head length (%SL)	31,2	25,6	27,8
Head depth (%HL)	78,6	62,1	69,2
Snout length (%HL)	36,2	26,4	33,3
Orbit diameter (%HL)	32,4	22,2	26,7
Postorbit length (%HL)	50,0	40,8	46,0
Interorbit length (%HL)	37,9	24,6	31,9
Predorsal length (%SL)	55,7	50,3	53,1
Postdorsal length (%SL)	49,7	44,3	46,9
Dorsal fin base (%SL)	15,7	12,1	13,8
Dorsal fin length (%SL)	24,0	18,9	21,0
Pectoral fin length (%SL)	22,7	18,3	20,6
Pelvic fin length (%SL)	19,3	15,6	17,5
Anal fin length (%SL)	21,7	15,7	18,1
Anal fin base (%SL)	13,9	9,8	11,9

Measurement		*Range*		
		Max.	Min.	$\overline{M}$
Body depth (%SL)		26,5	20,2	23,6
Body width (%SL)		18,3	12,0	15,5
Caudal peduncle length (%SL)		23,4	18,6	21,1
Caudal peduncle depth (%SL)		12,8	10,3	11,7
Anterior barbel length (%OD)		122,2	35,7	96,9
Posterior barbel length (%OD)		150,0	42,9	110,9
Pectoral–pelvic length (%SL)		26,5	10,0	23,5
Pelvic–anal length (%SL)		21,2	15,2	18,2
Pharyngeal bones L/W	(N = 21)	5,7	4,4	4,9
Length of intestine (%SL)	(N = 58)	102,3	57,6	80,8

Meristics	
Dorsal fin rays	iii–iv (iv) + 7–8 (8)
Anal fin ray.	ii–iv (iii) + 6–8 (7)
Pectoral fin rays	11–16 (14–15)
Pelvic fin rays	7–8 (8)
Total vertebrae	36–39 (37–38)
Precaudal vertebrae	18–20 (19)
Caudal vertebrae	17–20 (18–19)
Predorsal vertebrae	11–13 (12)
Preanal vertebrae	20–22 (21)
Supraneurals	6–8 (7)
Lateral line scales	35–40 (37–38)
Caudal peduncle scale rows	15–19 (16)
Scale rows lat. line–dorsal	5–9 (6)
Scale rows lat. line–pelvic	3–5 (4)
Scale rows lat. line–anal	3–5 (4)
Predorsal scale rows	14–21 (15–17)
Primary scale radii ($\overline{M}$ to nearest whole no.)	13
Pharyngeal teeth (mode)	2, 3, 4–4, 3, 2

The body is completely covered with cycloid scales that are only moderately reduced in size anteriorly between the pectoral fins. A small triangular pelvic axil scale is present. Scales are radiately striated with about 13 striae from an anteriorly displaced focus.

The dorsal fin originates over or just behind the origin of the pelvics. The last unbranched dorsal fin ray is segmented and flexible with vestigial serrations evident in some specimens. The posterior margin of this fin is straight or slightly concave. Pectoral fins are rounded, almost reaching the base of the pelvics. The pelvics are also rounded but do not reach the anterior base of the anal fin. The anal fin has a straight or slightly concave posterior margin. The caudal fin is forked with rounded lobes.

There are 2–3 + 6–9 short well spaced gill rakers on the anterior gill arch. The pharyngeal bones are falcate with a length to width ratio of 4,4–5,7. The pharyngeal teeth are in three rows,

2, 3, 4–4, 3, 2. The crowns are pointed in a conical cusp. The intestine is short, less than the SL, and has a single simple flexure.

Adults in breeding condition have numerous minute erupted tubercles (excresences) scattered densely and irregularly over the top and latero-dorsal surfaces of the head, over the exposed surface of the dorsal and latero-dorsal scales and in widely spaced single rows over the fin rays of all fins.

The general colour is pale brown to olive green with lighter ventral surfaces. The head is greenish brown with metallic silvery-gold on the opercula. The iris is silvery-gold and the pupil black. The barbels are dark and conspicuous. The fins are clear or hyaline with scarlet red basal portions (not always well expressed). Fin rays of the dorsal and caudal fins are brown. A more-or-less conspicuous unbroken dark lateral band runs from behind the head to the base of the caudal fin. In breeding condition both sexes (especially the males) become suffused with bright red.

The lateral line is complete and runs straight or follows a slightly curved path from the head to the end of the caudal peduncle. The cephalic lateral line system is complete without reductions or disjunctions. There is a short supra-preopercular tube on the opercle.

Distribution

This species is endemic to the Twee River and parts of its feeder tributaries, the Middeldeur and the Suurvlei Rivers (Fig. 45) (Skelton, 1974). There are a series of waterfalls on the Twee River and *B. erubescens* is not found below the first of these above the confluence of the Twee and the Leeu (Lion) River.

Notes on the breeding biology

The author has observed the spawning activities of this species on two occasions. On December 8, 1973 a large school of ripe running male specimens was netted from the open waters of a large pool of the Suurvlei River. The day was overcast and cool and it was raining intermittently. The second occasion was on October 14, 1983 below a small low level bridge on the Suurvlei River. A school of predominantly (at least 80%) male specimens was milling over the gravel next to a large rock in flowing water below a small cascade. Individual large females would join the milling school and were immediately closely attended by two or three males swimming up from below and behind and contacting the female in the vent region. Specimens of both sexes caught from the school were in ripe running condition. The weather on this occasion was sunny but a cold wind was blowing.

Conservation status

The Twee River redfin is a vulnerable species (Skelton, 1987) because of its very restricted distribution and deteriorating environment.

Etymology

The name *erubescens* refers to the red breeding colours of this species (Skelton, 1974).

DISCUSSION

The taxonomy of African freshwater fishes has, for the main part, entered a secondary phase of revision and consolidation of the primary or alpha phase of purely descriptive accounts. This present study of the redfin minnows is the third taxonomic revision of the group. It differs from the previous two (by Barnard (1938 and 1943) and Jubb (1965 and 1967)) by an analysis which concentrates on characters rather than on the species. This was necessary because the outstanding problems from the earlier revisions were those that required an understanding of the intra- and infra-specific variation of certain characters.

The taxonomic changes made by the study include the recognition and description of a new species *B. erubescens*, the resolution of interspecific boundaries between two species pairs (*P. burchelli* and *P. burgi*, and *P. afer* and *P. asper*), and the recognition of relationship between *P. quathlambae* and the Cape Fold redfin species. It is probably in regard to the last of the above-mentioned changes that the approach taken was most valuable i.e. the resolution of phylogenetic relationships of the species. Indeed the resolution of the outstanding taxonomic problems of the species was necessary before, and in turn allows for, the phylogenetic and zoogeographical investigations.

The results of the redfin study may be useful for comparison with other cyprinid groups in Africa. Redfin variability is possibly higher than most other African small *Barbus*-like cyprinid species. For example, many African small *Barbus* species have much more narrow ranges of scale counts (*vide* Greenwood (1962), Jubb (1967), Hopson (1965), Leveque (1985) etc.). This may relate to two factors considered by Nikolsky (1976), firstly that fishes at higher latitudes have in general a greater range of variability, and secondly, character variability in fishes is inversely proportional to the diversity of the fauna. For the redfins, higher latitude and lower faunal diversity are both in favour of greater variability of characters relative to other African minnows.

By concentrating on characters the study also allows a better appreciation of the distinctive features of the species and the groups. This is important for an understanding of the evolution of these minnows, about which little is known or has been written. Evolutionary aspects of the redfins will be discussed in relation to their phylogeny (Skelton, in prep. a).

The present study was instituted partly because of a conservation concern for the species. The conservation status of each species has been noted in the individual species accounts. A high proportion of the species are threatened to a varying extent; three *Pseudobarbus* species are endangered and two others are rare, *B. erubescens* is vulnerable and *B. calidus* is rare. The full reasons for the status of each species is given by Skelton (1987). One of the prime causes for the decline of the redfins is the introduction of alien predator fishes (Skelton, 1986).

Why has there been such a large impact on these particular fishes? The answer is not simple and many factors appear to be involved including the nature of the environment, the life history style of both prey and predator and Man-made changes to the environment. It is hoped that by clarifying the taxonomy of the species this study will assist the important process of the conservation of these attractive and interesting fishes.

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Description of a new species of *Heleophryne* Sclater, 1899 from the Cape Province, South Africa (Anura: Heleophrynidae)

by

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CONTENTS

ABSTRACT

A new species of ghost frog, genus *Heleophryne*, is described. *H. hewitti* **sp. nov.** is known only from the Elandsberg Mountains, Eastern Cape Province, South Africa. It is geographically isolated from *Heleophryne regis* and other *Heleophryne* populations in the southern Cape Province. Diagnostic features include a unique mating call and characteristic dorsal colour-pattern. It is considered to belong to the *H. purcelli/regis* species complex in the Cape Folded Mountain Belt. Certain morphological characters shared by members of this complex are identified and presented.

INTRODUCTION

At present four species of *Heleophryne* are recognised in South Africa; *H. purcelli* Sclater, *H. regis* Hewitt, *H. natalensis* Hewitt, *H. rosei* Hewitt (Boycott, 1982).

During a distribution survey of the genus *Heleophryne* in the Cape Province in October 1979, an isolated population was discovered in the Loerie and Otterford Forest Reserves in the Elandsberg Mountains 50 km WNW of Port Elizabeth. The nearest population of *Heleophryne* was over 65 km to the south-west of the Elandsberg range, and at that time referred to *H. purcelli regis* (*sensu* Poynton, 1964). This is now treated as a full species (Boycott, 1982). Between October 1979 and October 1980 comparative series of both populations were collected.

During this period tape recordings of the mating calls of *H. regis* and the new population were made at several localities. They indicate that the two populations represent distinct species.

MATERIALS AND METHODS

Specimens are lodged in the following institutions (abbreviations in parenthesis): Albany Museum, Grahamstown, South Africa (AMG A); British Museum (Natural History), London, England (BMNH); Museum of Comparative Zoology, Harvard, U.S.A. (MCZH A); Natal Museum, Pietermaritzburg, South Africa (NM); Port Elizabeth Museum, Port Elizabeth, South Africa (PEM A); South African Museum, Cape Town, South Africa (SAM); Transvaal Museum, Pretoria, South Africa (TM).

Tape recordings of mating calls were made in the field using a Philips N2203 port ole cassette recorder, and analysed on a sound spectograph (Kay 7029A spectrum analyser) within the frequency range 80–8000 Hz using a wide-band (300 Hz) filter.

To assist with colour-pattern description specimens were photographed in detail before preservation. They were killed in 70% ethyl alcohol, partially dissected for sex determination, carefully set, and then placed in 10% formalin for long-term preservation.

The following measurements were recorded: snout-vent length—tip of snout to vent (SV); hindlimb length—vent to tibio-tarsal fold (HL); width of head—measured at widest point (HW); depth of snout—measured anterior to orbits (DS); diameter of eye—distance between anterior and posterior corners (DE); internarial distance—distance between the nostrils (IN); inter-orbital distance—distance between the anterior corners of the eyes (IO); tibia length—measured when the shank is compressed between the femur and tarsus (Tib); tarsus—tibio-tarsal fold to tip of 4th toe (Tar); whole hindlimb length—vent to tip of 4th toe (WH).

DESCRIPTION

Heleophryne hewitti sp. nov.

Fig. 1.

Type locality

Upper reaches of the Geelhoutboom River, Loerie Forest Reserve, Elandsberg Mountains (3325 CC Loerie), Eastern Cape Province, South Africa. This river is a clear, swift-flowing, rocky, perennial mountain stream (Fig. 2).

Holotype

Adult male (AMG A 621), collected by R. C. Boycott at 23h00 on 17 October 1979 beneath a partially submerged rock at the type locality (33°47′54″S, 25°03′43″E. Alt. 420 m).

Paratypes

Twenty adult males and six adult females, of which four are gravid (AMG A 697; BMNH 1981.8; PEM A 458; TM 55206), collected between 10 October 1979 and 30 October 1980 from four localities: the type locality (AMG A 613, 695, 696, 697, 698; BMNH 1981.7, 1981.8; MCZH A 100155; NM 6770; PEM A 458, 459; SAM 45185; TM 55203, 55204, 55205, 55206); Martins River (AMG A 699; PEM A 460; SAM 45187; TM 55207); Klein River (AMG A 622; MCZH A 100156; NM 6771; PEM A 461; TM 55208) and Diepkloof River (AMG A 694). All were collected beneath submerged and partially submerged rocks, or near cascades by Athol Jones, Dean Smith-Belton and Richard Boycott.

Diagnosis

Maxillary teeth present. Vomerine teeth in two raised transverse rows between the choanae, the distance between the two rows is greater than the distance from the edges of the

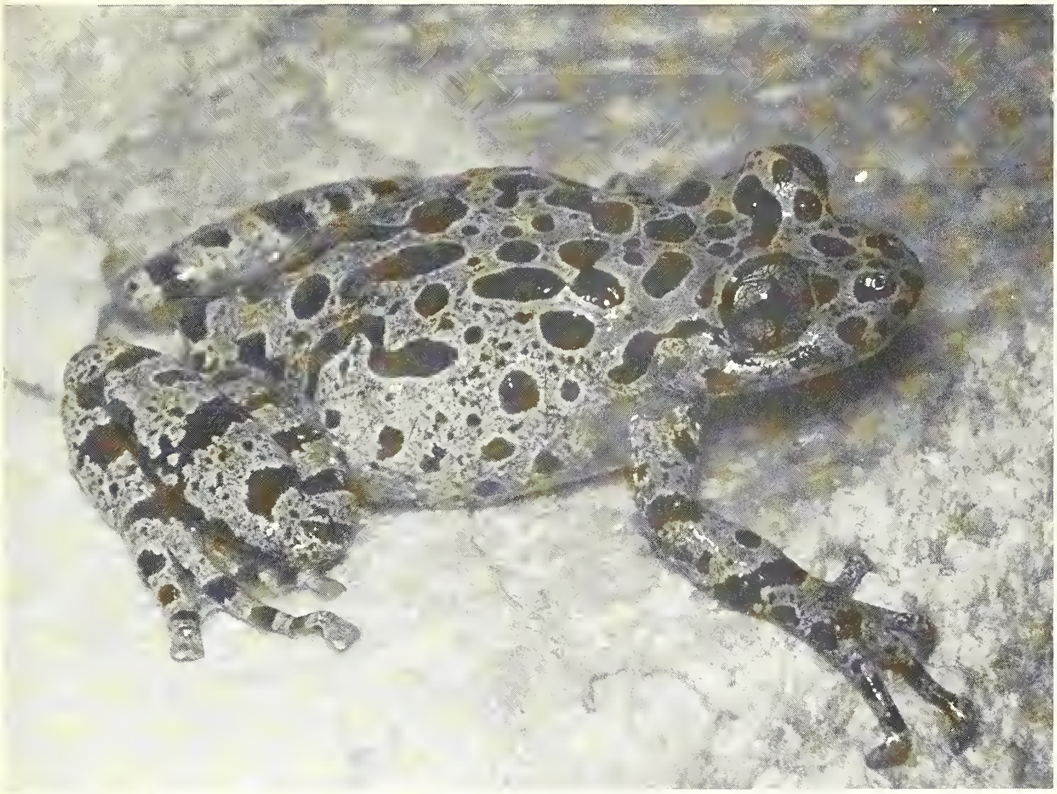

Fig. 1. *Heleophryne hewitti* sp. nov.—adult female specimen (AMG A 697) from the type-locality (3325CC Loerie).

choanae to the edges of the tooth rows. Internarial distance greater than half the interorbital distance. An Eastern Cape Province form, endemic to the Elandsberg range; of moderate size (larger than *H. regis*) with a maximum SV length of 50,3 mm (females), 47,0 mm (males); a unique mating call, each note with a duration of from 0,06 to 0,11 seconds; a characteristic dorsal colour-pattern; and more extensive webbing than *H. regis*, males have webbing to the tip of the fifth toe, females have only one phalanx of the fifth toe free of webbing.

Description of holotype

Supratympanic fold distinct, tympanum hidden. Webbing extends to the tip of the fifth toe and $2^1/_2$ to 3 phalanges of the fourth toe are free of webbing. Snout-vent length subequal to hindlimb length (SV/HL ratio 1,07). Width of head 69% of tibia length. Distance from vent to tibio-tarsal fold 60% of whole hindlimb length. Internarial distance greater than half the interorbital distance (IN/IO ratio 0,55). Diameter of eye subequal to internarial distance (DE/IN ratio 1,04) and greater than depth of snout (DE/DS ratio 1,11). Fingers relatively long (iii > iv > ii > i), unwebbed and with well developed subarticular tubercles. Toes long (iv > iii > v > ii > i), webbed and with well developed subarticular tubercles.

Fig. 2. The type locality of *Heleophryne hewitti* sp. nov.—the upper reaches of the Geelhoutboom River in the Elandsberg Mountains (3325CC Loerie).

In life the dorsal pattern consists of numerous rounded and irregularly-shaped, dark-brown patches superimposed on a uniform light-brown to olive-brown background. The patches are marginated with a thin white line and are not interlinked. Numerous small spots and flecks of a similar colour are present between the larger patches. The hindlimbs are marked with dark, irregularly-shaped transverse bands that lack the white borders of the dorsal patches but remain distinct. Similar bands are present on the forearm, tarsus and outer fingers and toes. The nostrils are hidden in small, dark-brown spots; and there is no interorbital bar.

The forearms are slightly swollen and bear elongated nuptial pads. Dorsal skin folds are present but poorly developed. Asperities on the inner surfaces of the forearms are indistinct. Asperities are absent on the outer edges of the upper and lower jaws, and in the chest region.

Measurements of holotype

SV 47,0 mm; HL 44,1 mm; HW 16,5 mm; DS 4,4 mm; DE 4,9 mm; IN 4,7 mm; IO 8,6 mm; Tib 24,0 mm; Tar 32,7 mm; WH 73,1 mm.

Description and variation of paratypes

Range in snout-vent length 38,0–46,7 mm in males ($\bar{x}$ 41,6), 42,2–50,3 mm in females ($\bar{x}$ 44,6). Range in hindlimb length 38,5–46,8 mm in males ($\bar{x}$ 41,4), 41,3–47,1 mm in females ($\bar{x}$ 42,8). Morphometric data (ratios) obtained from paratypes: SV/HL 0,94–1,05; SV/Tib 1,74–1,96; SV/HW 2,55–2,79; Tib/HW 1,37–1,54; HW/DE 3,27–3,89; HW/IO 1,79–2,08; IO/DE 1,59–2,04; IN/IO 0,49–0,56; DE/IN 0,93–1,14; DE/DS 0,88–1,18. In 80,9% of males the snout-vent length was equal to or greater than hindlimb length (SV/HL ratio 0,94–1,07), and in all females it was greater (SV/HL ratio 1,02–1,07). In all paratypes the internarial distance was equal to or greater than half the interorbital distance (IN/IO ratio 0,49–0,56).

In males, 2 or 2½ phalanges of the fourth toe are usually free of webbing. However, in the holotype and one paratype (AMG A 699), the webbing extends to a point between 2½ and 3 phalanges from the tip. Females have 3 to 3½ phalanges of the fourth toe free of webbing. The webbing in males extends to the tip of the fifth toe or to a point within half a phalanx of the tip (SAM 45187); in *H. regis* it frequently falls short of the tip. In females 1 phalanx of the fifth toe is usually free of webbing, but in the largest specimen (PEM A 459) it extends to the tip; female *H. regis* usually have 2 phalanges of the fifth toe free of webbing.

The colouration of the paratypes is similar to that of the holotype. Colour-pattern polymorphism is absent and there is no colour-pattern difference between males and females. Variation in dorsal colour-pattern is minimal. It is mostly evident in the tone and contrast of the markings described for the holotype. A continuous interorbital bar, often formed by a series of interlinked blotches, is present in thirteen of the paratypes including all the females. The background colour of live specimens varies from yellow-brown to olive-brown; during the day a few specimens were seen and they had a dull green background colour. Lighter shades are more evident after dark. As in the holotype, all paratypes are very spotted with numerous smaller spots and flecks scattered between the larger dorsal patches, a condition not found in any of the *H. regis* specimens. The transverse bands on the limbs are distinct, these are usually indistinct or absent in *H. regis*.

Mating call

Recordings were made at the type locality at night and during the day on 3 and 4 October 1980. The call consists of a sequence of soft repetitive whistles. Each call sequence consists of 8 or 9 whistles. The interval between successive notes varies from 1,0 to 2,0 seconds, 1,5 seconds being the most common. Two second intervals were recorded during the day (11h00, air temperature 26,0° C; water temperature 16,8° C), but after dark (21h00, air temperature 10,0° C; water temperature 12,5° C) 1,0 and 1,5 second intervals were more common. Pauses between each calling sequence varied from 6,0 to 9,0 seconds. Often each calling sequence, particularly those separated by 8,0 or 9,0 second pauses, commenced with a long, loud note produced as a drawn out whistle (Figs 3a and 3c). This may have a duration of almost 0,25 seconds (Fig. 3c), although it is usually between 0,15 and 0,2 seconds long.

Successive whistles in the sequence are of considerably shorter duration, varying from 0,06 to 0,11 seconds. They are distributed over a narrow frequency range 1,7–2,2 kHz (Figs. 3a and 3b). The call of *H. regis* is distributed over a much wider frequency range, between 1 and 2,6 kHz (Boycott, 1982). The initial drawn-out part of the call, as indicated in Figs 3a and 3c, commences at a higher frequency (2,0–2,2 kHz) and sweeps slightly downward.

Etymology

This species is named after Dr John Hewitt (1880–1961) in honour of his remarkable contributions to South African herpetology.

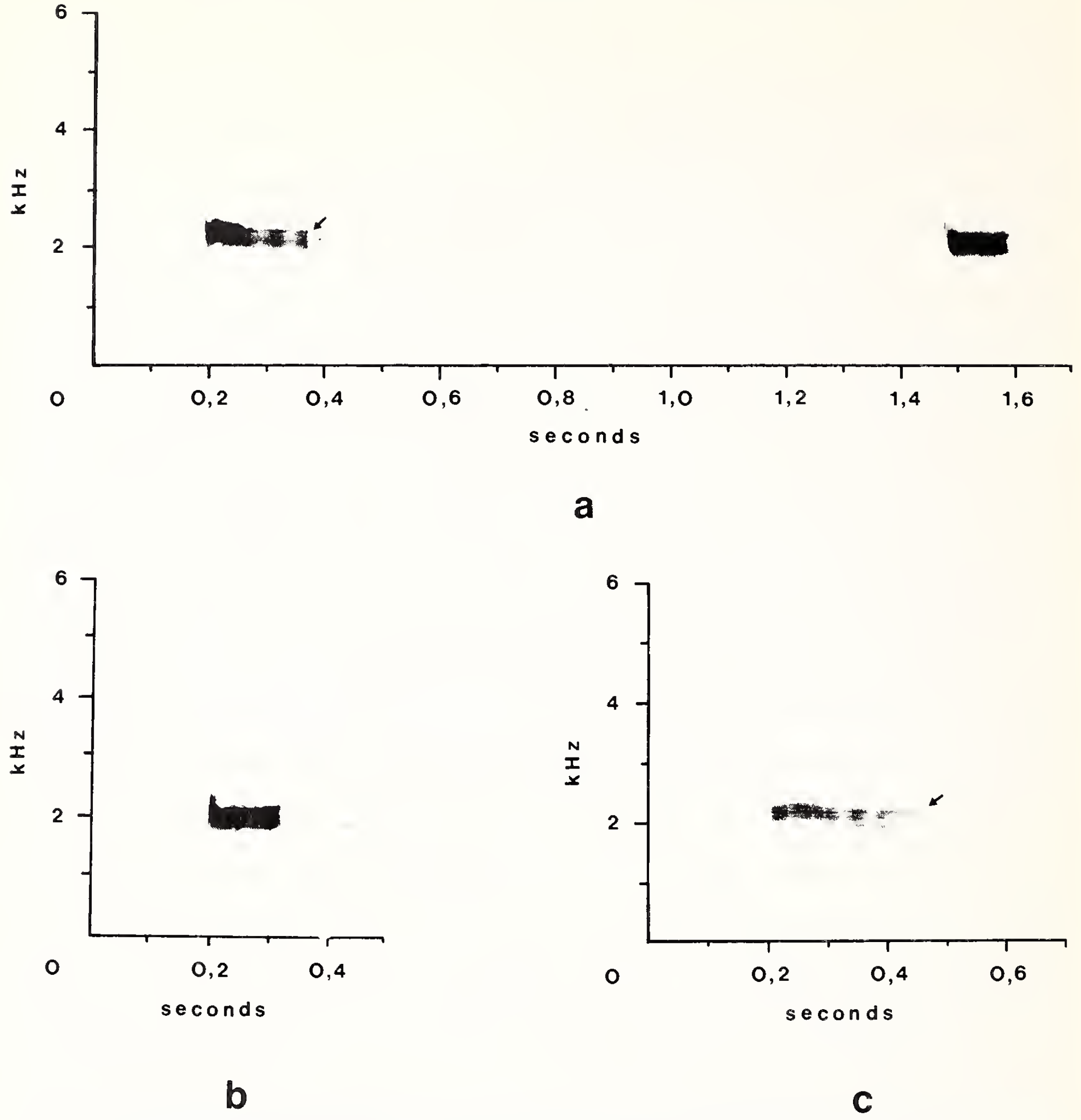

Fig. 3. Sonograms of the mating call of *Heleophryne hewitti* sp. nov. showing: (a) the initial drawn out note and first whistle of a calling sequence; (b) a whistle from a calling sequence; (c) an initial drawn out note.

ADDITIONAL MATERIAL

Tadpoles and eggs. The tadpoles and eggs of *Heleophryne* are quite different from those of other southern African amphibians. The tadpole's most distinctive characteristic is its unique suctorial mouth, which extends right across the ventral surface of the head. Numerous transverse tooth-rows are present, four rows on the upper jaw and more than a dozen on the lower jaw. The

number of tooth rows depends on the age of the tadpoles (*pers. obs.*). The eggs of *Heleophryne* are as distinctive as the tadpoles, being bright yellow and large yolked.

Tadpoles and eggs of *H. hewitti* **sp. nov.** were collected from various localities. Tadpoles were collected from the type-locality (three series—PEM A 463; SAM 45181, 45182); Martins River (two series—AMG A 719; PEM A 464); Klein River (eight series—AMG A 628, 629; NM 6772, 6773; PEM A 462; SAM 45183, 45184; TM 55202); and Diepkloof River (three series—AMG A 630; TM 55200, 55201). Eight egg batches have been found, six at the type locality and two in the Klein River. The early development of four batches was observed and samples were preserved at different stages (three from the type locality—AMG A 614; SAM 45190, 45191; and one from the Klein River—NM 6775). The total number of eggs in four batches was counted, these do not necessarily refer to the sampled batches as some were counted *in situ* and left. Assuming that none was overlooked, these totalled 93, 103, 120 and 150. Six egg batches were found in October 1979 and two in October 1980.

Most oviposition sites were located beneath submerged or partially submerged rocks of variable size. These were usually in relatively quiet backwaters where the stream flow was not very rapid and the water depth varied from 20 to 60 cm. However, one batch was found under a semi-submerged rock in the middle of a shallow (20 cm), rapidly flowing section of the stream. Indeed, when the rock was lifted most of the eggs were swept away by the current. The eggs have a surprisingly hard capsule which probably protects them should they be dislodged from the original oviposition site. The eggs and oviposition sites of *H. hewitti* are comparable to those of *H. purcelli* as described by Visser (1971) and Boycott (1972).

HABITAT, DISTRIBUTION AND CONSERVATION

It is generally accepted that the tadpoles of *Heleophryne* spend at least two seasons in the rivers and streams before metamorphosing and the genus is therefore prevented from colonizing non-perennial streams (Rose, 1926; Wager, 1965; Boycott, 1982; Boycott and de Villiers, 1986). The breeding season of *H. purcelli* and *H. regis* (Boycott, 1982) and *H. hewitti* coincide with that time of the year when river flow is reduced. This strategy enhances the survival chances of eggs and young tadpoles at a critical stage of their development. Furthermore, it ensures the longterm survival of tadpoles as any stream that has water at that time of the year will certainly be perennial.

The Van Stadensberg Mountains form a south-easterly extension of the Elandsberg Mountains and as they are continuous they are here referred to collectively as the Elandsberg range. The highest peaks in the Elandsberg range, Stinkhoutberg (1 106 m) and Elandsrivierberg (987 m), receive 1 000 mm of rain per annum. The Elandsberg range has a higher annual rainfall than the Groot Winterhoek range situated to the north and throughout its length several perennial streams are present.

Extensive surveys in the Elandsberg range have revealed that *H. hewitti* has a very limited distribution in these mountains. The species is restricted to four rivers, the Geelhoutboom River, Martins River, Klein River (all 3325CC Loerie) and Diepkloof River (3324DB Cockscomb/3324DD Hankey). Two of these, the Martins River and Klein River, have perennial tributaries which the other two lack. The sources of the four rivers extend over a distance of just 10 km, and the greatest distance separating any two of these rivers is 3,5 km. All these localities are between 400 m and 550 m above sea level, and are clear, swift-flowing, perennial mountain streams with rocky beds. The banks along the streams are generally steep and thickly vegetated but not forested (Fig. 2). They resemble more closely the typical habitat type of *H. purcelli* and not that of *H. regis*. The indigenous vegetation of the Elandsberg range is classified as False Macchia (Acocks, 1975). However, due to the high rainfall most of the mountain slopes have been afforested and very little of the natural vegetation remains.

Investigations were carried out in six other river systems throughout the Elandsberg range. These are the Honey Clough River (Otterford Forest Reserve), Berg and Bulk rivers (Longmore Forest Reserve), Van Stadens River (Van Stadens Forest Reserve), Keurkloof River (Loerie Forest Reserve) and the Sand River (Hankey Forest Reserve). No *Heleophryne* specimens were found at any of these localities which emphasises the geographical isolation of the *H. hewitti* population. The distribution of the species is shown in Fig. 4.

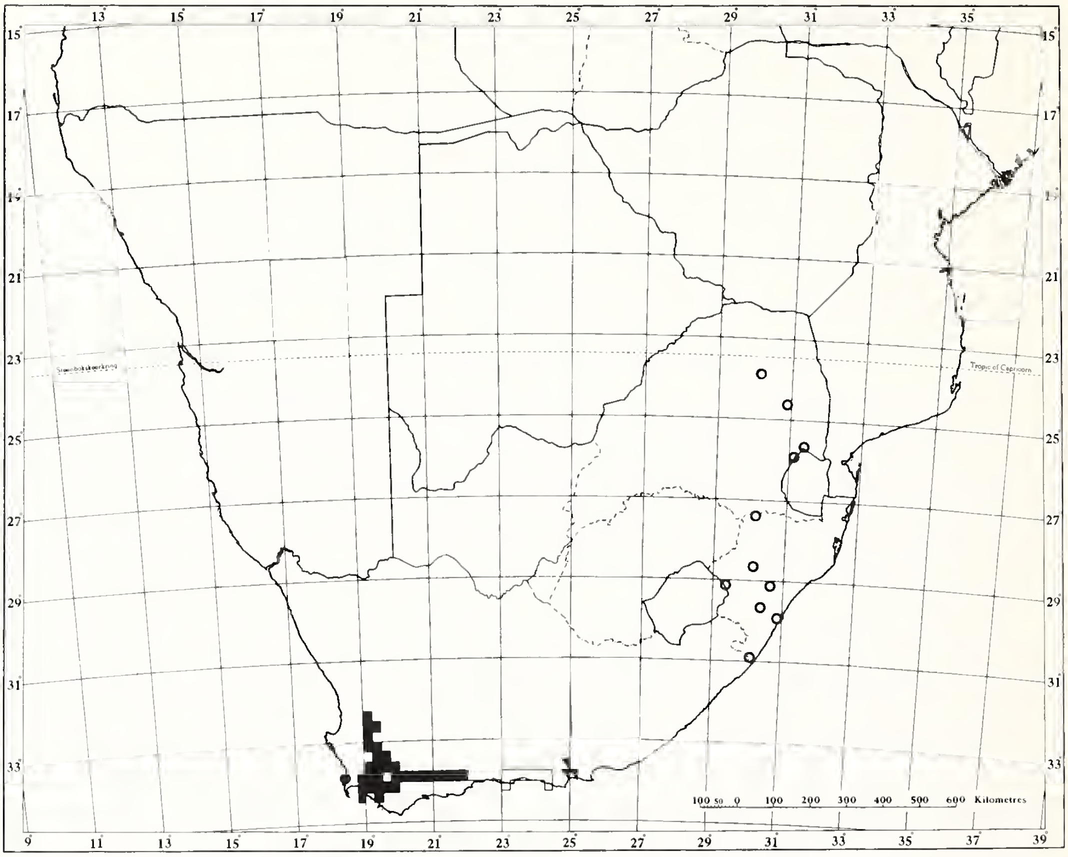

Fig. 4. The distribution of *Heleophryne* Sclater in South Africa.

● *Heleophryne rosei* Hewitt ■ *Heleophryne purcelli* Sclater
□ *Heleophryne regis* Hewitt ■ *Heleophryne hewitti* sp.nov
○ *Heleophryne natalensis* Hewitt

H. hewitti appears to have one of the most restricted distribution ranges of any southern African amphibian. Over the last six or seven years through a combination of unwise forestry practices, severe fires and floods, the habitat of *H. hewitti* is now seriously threatened. In the early 1980s fires devastated the Otterford and Loerie plantations and most of the trees were left

standing. In June 1986 these were cleared and within months, as a result of heavy rain, flooding led to the extensive silting up of the streams, particularly the Geelhoutboom River—the type locality. As a result of this, large tracts of the type locality have been rendered uninhabitable for*H. hewitti* and at present the habitat hardly resembles that depicted in Fig. 2 (W. R. Branch *pers. comm.*).

Another threat to the continued survival of this species would be the introduction of exotic fish species into the streams. This has already occurred in the Honey Clough River and in some of the other rivers on the periphery of the species' distribution range (*pers. obs.*). It is not known whether the construction of dams and reservoirs in those streams, such as the Bulk River and Sand River, on the northern side of the Elandsberg range has affected the distributon of *H. hewitti*. However, dams constructed at higher altitudes (i.e. in areas where the species does occur) will certainly reduce the amount of suitable habitat available to the species.

COMPARISON WITH OTHER SPECIES

In the Cape Province because of the isolated nature of the mountain ranges one can expect considerable taxonomic complexity. Attention was initially drawn to this by Poynton and Broadley (1978). More recently, the findings of the present author appear to substantiate this dictum (Boycott, 1982).

Heleophryne natalensis and *H. rosei* are well separated morphologically from the other species of ghost frog in the Cape Province, possibly due to their geographical separation (Poynton, 1964). The Cape Province populations of *Heleophryne* (excluding *rosei*) share certain morphological characteristics including secondary sexual characters, dorsal pattern and eye markings. They form a distinct group—the *H. purcelli*/*H. regis* species complex.

During the breeding season both sexes develop secondary sexual characters (Boycott, 1982). In males these include the development of loose dorsal skin folds, swollen forearms (nuptial pads), and asperities or spines. The distribution and concentration of asperities or spines can be useful species characters (Boycott, *op. cit.*). There is a marked difference in the structure, distribution and concentration of the asperities in *H. natalensis, H. rosei* and in members of the *H. purcelli*/*H. regis* complex. In *H. natalensis* 'jagged', conspicuous spines are present, and restricted to the axilla and the dorsal aspect of the first three fingers. This is well illustrated in Passmore and Carruthers (1979). However, in *H. rosei, H. purcelli* and *H. regis* these structures can be more aptly termed asperities as they are considerably smaller in size, more numerous and widely distributed over the entire dorsal surface. The asperities on the forelimbs in *H. rosei* are concentrated on the outer surfaces of the forearms, whereas in *H. purcelli, H. regis* and *H. hewitti* they are restricted to the inner and dorsal surfaces of the forearms. Despite the relatively large series of specimens examined (n = 27), it was discovered that the asperities in *H. hewitti* do not appear to be as well developed nor as conspicuous as they are in *H. purcelli* and *H. regis*. Nonetheless, the distribution and concentration of asperities in the new species conform more to the typical pattern found in *H. purcelli* and *H. regis*.

H. natalensis and *H. rosei* possess a distinctly mottled dorsal pattern, the actual size and shape of the dorsal patches being somewhat ill defined. Individuals representative of the *H. purcelli*/*H. regis* complex possess clearly defined, vivid, dorsal patches which are usually bordered by thin lines. All members of the genus possess vertically elliptic pupils which in some are well concealed due to the presence of dark pigment in the eye. *H. natalensis* and *H. rosei* lack the dark, transverse band through the eye that is always present in members of the *H. purcelli*/*H. regis* complex. The possession of clearly defined dorsal patches and a dark transverse band through the eye by *H. hewitti* clearly indicate that this species is part of the *H. purcelli*/*H. regis* species complex in the Cape Folded Mountain Belt.

Unfortunately most of the preserved material of *H. natalensis* could not be examined by the author. Five specimens (TM 14927, TM 21066, TM 21067, TM 21413, TM 26204) are old, fragile and preserved in such awkward positions as to be unmeasurable. Fresh *H. natalensis* material is needed. Morphometric data obtained from samples of *H. rosei* (n = 10); *H. purcelli* (n = 25); *H. regis* (n = 25) and *H. hewitti* (n = 27) revealed few diagnostic differences between the species (Table 1). It appears that the snout-vent length in *H. rosei* is equal to or less than the hindlimb length (SV/HL ratio 0,93–1,05; $\bar{x}$ 0,99), whereas in the other species it is normally equal to or greater than the hindlimb length (Table 1). Furthermore, in *H. rosei*, unlike the other Cape species, the internarial distance is less than half the interorbital distance (IN/IO ratio 0,45–0,52; $\bar{x}$ 0,48); and the tibia is usually one and a half times the width of the head (Tib/HW ratio 1,43–1,56; $\bar{x}$ 1,50). These ratios may be useful diagnostic characters and should be tested when more *H. rosei* and *H. natalensis* material becomes available. *H. rosei* can be separated from the other Cape species on the basis of the ratios SV/HL; Tib/HW; and IN/IO (Table 1). The three species representatives of the *H. purcelli*/*H. regis* complex are clearly very similar to one another and cannot be separated on morphometric grounds. However, vast differences exist between the mating calls.

Table 1.

Morphometric data for species of *Heleophryne*

	H. rosei n = 10			*H. purcelli* n = 25			*H. regis* n = 25			*H. hewitti* **sp. nov.** n = 27		
Ratio	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.
SV/HL	0,93–1,05	0,99	0,04	0,93–1,11	1,02	0,04	0,95–1,16	1,01	0,05	0,94–1,07	1,02	0,03
Tib/HW	1,43–1,56	1,50	0,05	1,25–1,53	1,40	0,07	1,37–1,54	1,46	0,05	1,37–1,54	1,46	0,05
HW/IO	1,83–2,07	1,93	0,09	1,87–2,19	2,00	0,09	1,75–2,15	1,90	0,09	1,79–2,08	1,92	0,08
IN/IO	0,45–0,52	0,48	0,02	0,44–0,58	0,52	0,03	0,47–0,61	0,54	0,03	0,49–0,56	0,53	0,02
DE/IN	0,91–1,20	1,05	0,10	0,94–1,24	1,07	0,07	0,88–1,13	0,99	0,05	0,93–1,14	1,01	0,06

A detailed study of the tadpoles of *Heleophryne* from the Cape Province (Channing *et al.*, in prep.) has revealed that most of the sampled populations are distinguishable on a suite of morphological characters. Although the tadpoles of the southern Cape populations are similar, nostril morphology, pigmentation, tail length and proportions suggest that the taxonomic status of other isolated populations, for example on the Kammanassie Moutains, the Baviaanskloof Mountains and the Kouga Mountains warrants further investigation. The tadpoles of *H. hewitti* can be distinguished from those of *H. regis* on nostril morphology, tail length and proportions.

Distance between populations has been demonstrated on more than one occasion to mean reproductive isolation, even when morphological difference is not great. Therefore as the population under discussion is separable on mating call and tadpole morphology and no intergrades are known to occur in nature, it is proposed that this population be considered specifically distinct. The most diagnostic feature of any frog species is the voice (Blair, 1958; Pengilley, 1971; Littlejohn, 1971; Passmore and Carruthers, 1975; Passmore and Carruthers, 1979; Passmore, 1981; Telford and Passmore, 1981; Boycott, 1982). Examination of the sonograms of the calls of *H. purcelli* and *H. regis* (Boycott, 1982) and *H. hewitti* (Fig. 3) shows clearly that call difference alone can be used to separate these species unequivocally from each other.

ACKNOWLEDGEMENTS

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Three new South African species of *Aulacoderus* la Ferté, a subgenus of *Anthicus* Paykull (Coleoptera: Anthicidae)

by

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(Department of Zoology and Entomology, Rhodes University, Grahamstown)

ABSTRACT

Descriptions and figures are given of three new species of *Anthicus (Aulacoderus),* namely *halleyi, tardus* and *propinquus*, and their relationships to other species are discussed.

INTRODUCTION

The present paper constitutes a third supplement to the author's monograph of *Aulacoderus* (van Hille, 1984) adding three new species. The two previous supplements (van Hille, 1985a and 1985b) added thirty-eight and six species respectively. An additional three species of *Aulacoderus* were described in a paper on Anthicidae collected in Botswana (van Hille, 1986).

TAXONOMIC DESCRIPTION AND DISCUSSIONS

SECTION 5

Anthicus (Aulacoderus) halleyi **spec. nov., Figs 1–4**

Size. Length 2,45 mm (1,70–2,62); width over broadest part of elytra 0,81 mm (0,70–0,93).

Head (Fig. 2). Matt; testaceous to dark testaceous; posterior arch broadly round. Punctures close together, each surrounded by a round lighter area; with short procumbent hairs. Eyes rather small and somewhat bulging.

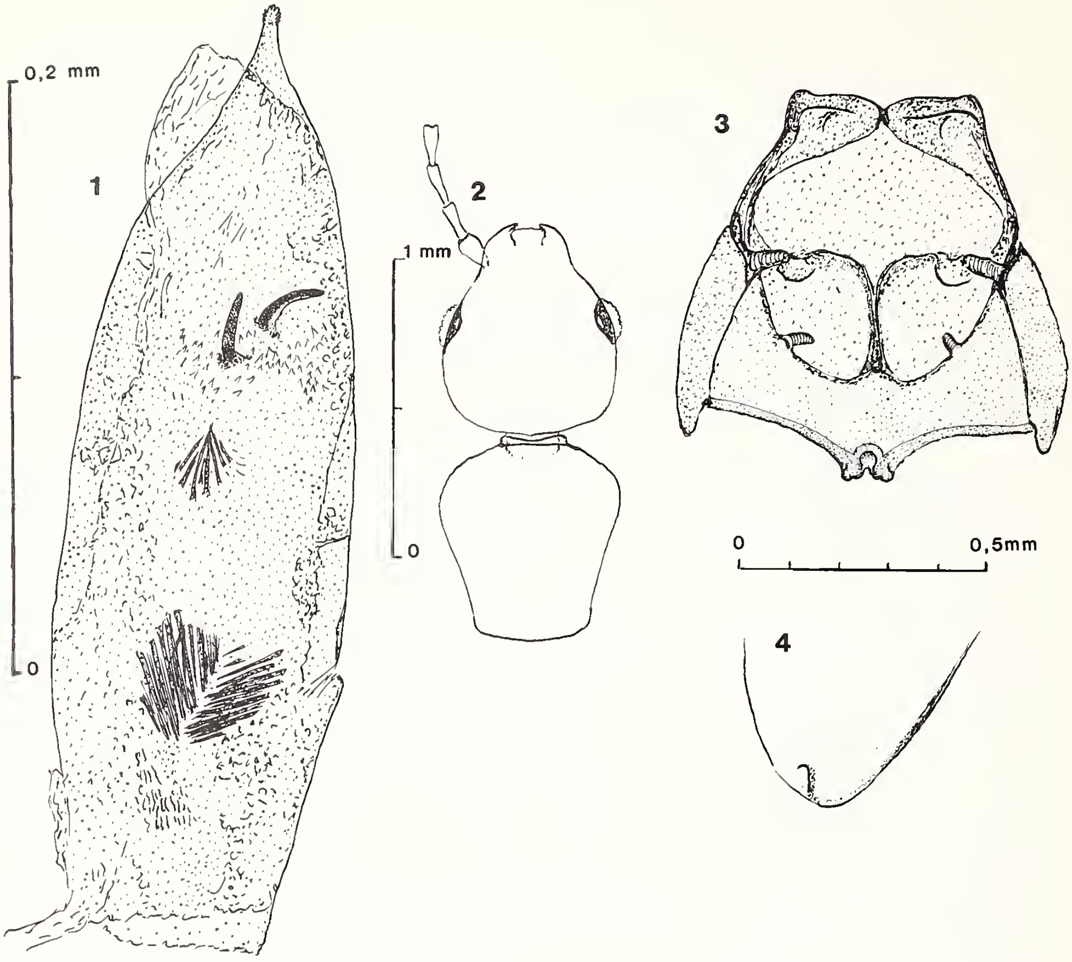
Prothorax (Fig. 2). Matt; testaceous; longer than broad, slightly broader than head. Punctures as on head, with short recumbent hairs. Without basal lateral constrictions.

Elytra. Matt; testaceous, slightly lighter than prothorax. Punctures minute, not surrounded by a lighter area, with fine recumbent hairs, longer than on prothorax. In male not apically pointed (Fig. 4) but with a somewhat elongated notch.

Wings. Absent; metatergum hardly sclerotised.

Antennae. Slender; light testaceous. Toward apex hardly broadened and not darker. Apical segment somewhat longer than penultimate segment.

Undersurface. Light testaceous. With mesepimerite apophyses with spiral markings and a smaller pair of apophyses with spiral markings on anterior margin of metasternum (Fig. 3) projecting into the mesocoxal cavities. Metepisterna immovably fused onto metasternum.



Figs 1–4. *A.* (*A.*) *halleyi* spec. nov. 1: aedeagus. 2: head and prothorax. 3: meso- and metathoracic sterna. 4: apex of elytron of male. Figs 3 and 4 at same magnification; other figs as indicated.

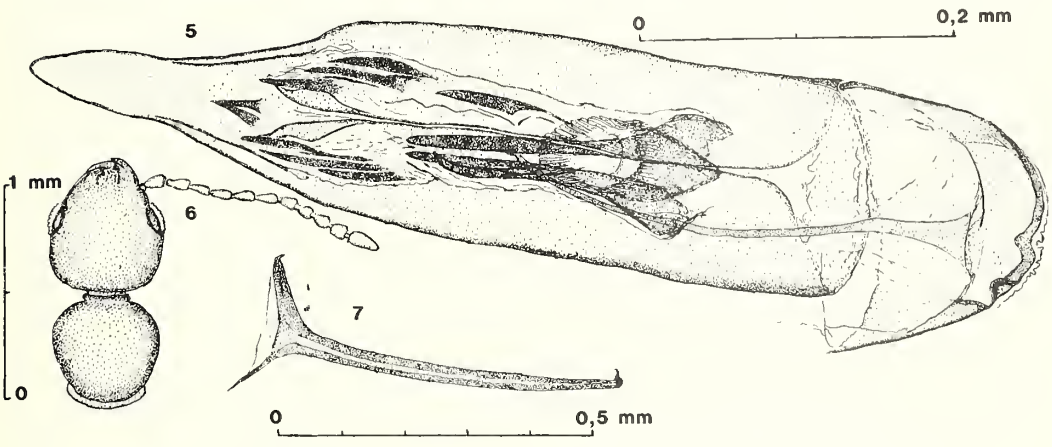
Male abdomen. Aedeagus (Fig. 1). Tegmen slightly sclerotised, with pointed apex; median lobe membranous; in the preparation it cannot be seen as a structure separate from the connecting membrane. Genital opening invisible. The connecting membrane has a number of sclerotised structures: a pair of proximal groups consisting of 12 to 15 straight spines each; the spines are pointed at the median end and point obliquely inward and proximally; more distally lies a single group of 8–10 similar spines pointing inward and distally; subapically lies a pair of short broad dark claws, surrounded by a field of very small thorns which are not pigmented and probably not sclerotised. Spiculum gastrale with a pair of short asymmetrical arms. Last exposed sternum somewhat long, with rounded apex. Last exposed tergum trapezoidal.

MATERIAL EXAMINED. South Africa: near old Storms River Bridge, 33° 59′S, 23° 55′E, 25.ii–3.iii.1986, Holotype ♂, Paratypes 1205 (probably all ♂♂), (J. C. van Hille); Wit River Gorge, 33° 39′S, 24° 31′E, 14–16.x.1986, Paratypes 7 (probably all ♂♂), (F. C. de Moor). Most of the specimens from the first locality were collected at the camp site on the right side of the river but a number were taken in the forest on the mountain slope and along the road. At both localities all the specimens were collected on meloid bait and are consequently probably all males. The material is in the Albany Museum, Grahamstown.

This species has a number of peculiar features. Although the total absence of basal constructions of the prothorax is also found in *A. (A.) pici* (van Hille, 1984) in Section 15, the relationship is with a group of species in Section 5. This Section is characterised by the possession of parallel sclerites in the aedeagus. The group has been discussed (van Hille, 1985a) and includes the species *A.* (*A.*) *apterus*, *A.* (*A.*) *sebastiani*, *A.* (*A.*) *oosthuizeni*, *A.* (*A.*) *apophysialis* (all in van Hille, 1985a) and *A.* (*A.*) *vandersteli* (van Hille, 1985b). The members of this group possess a combination of all or several of the following features: dark elytra without colour pattern; absence of wings; speculum gastrale with short asymmetrical arms; lateral basal constrictions of prothorax indistinct or absent; in addition to the mesepimerite apophyses there is a pair of apophyses on the front margin of the metasternum; the metepisterna are immovably fused onto the metasternum; the connecting membrane of the aedeagus has two separate rows of teeth which are modified in many of the species. *A.* (*A.*) *apterus* has well developed parallel sclerites; in most of the other species in this group the parallel sclerites are much modified e.g. in *A.* (*A.*) *oosthuizeni*, *A.* (*A.*) *apophysialis* and *A.* (*A.*) *vandersteli*. *A.* (*A.*) *halleyi* has no parallel sclerites unless the pair of basal groups of spines is considered to be homologous with parallel sclerites.

A. (*A.*) *halleyi* has the first six of the seven special features of this special group of species. In some of the species the two rows of teeth are reduced and modified. In *A.* (*A.*) *apophysialis* two pairs of spines have been interpreted as a modification of the two rows of teeth. Thus in *A.* (*A.*) *halleyi* the pair of subapical claws may be the only remnant of the rows of teeth.

The median group of spines of *A.* (*A.*) *halleyi* is peculiar but in *A.* (*A.*) *vandersteli* the spines are not strictly arranged in pairs.



Figs 5–7. *A.* (*A.*) *tardus* spec. nov. 5: aedeagus. 6: head and prothorax. 7: speculum gastrale.

Anthicus (Aulacoderus) tardus **spec. nov., Figs 5–7**

Size. Length 2,43 mm (2,25–2,63); width over broadest part of elytra 0,86 mm (0,75–0,95).

Head (Fig. 6). Glossy; black; posterior arch broadly rounded. Punctures minute with short fine procumbent hairs. Eyes somewhat bulging.

Prothorax (Fig. 6). Glossy; dark testaceous to black, slightly lighter than head; longer than broad, slightly narrower than head. Without basal lateral constrictions but with a narrow basal margin. Punctures more distinct than on head with longer recumbent hairs.

Elytra. Glossy; dark testaceous to black. Punctures fine with fine recumbent hairs. In male with short round apical notch.

Wings. Absent; metatergum hardly sclerotised.

Antennae (Fig. 6). Slender, light testaceous. The apical five segments somewhat broader than the basal segments but not darker. Last segment longer than penultimate segment.

Legs. Testaceous; coxae and femora somewhat darker, tarsi somewhat lighter.

Undersurface. Meso- and metasternum very similar to those of *A.* (*A.*) *halleyi*, with similar apophyses and fusion of the metepisterna to the short metasternum. First abdominal sternum with a pair of very short round apophyses on anterior margin.

Male abdomen. Aedeagus (Fig. 5): Tegmen elongate, narrowing over distal third to a roundly pointed apex; not subdivided into an apical and a basal area; median lobe short, triangular with large, wide-open genital opening with striated margin; connecting membrane with six pairs of dark spines: the most proximal and largest pair of spines have a broad base which lies on either side of the base of the median lobe and extend over almost half of their length beyond the genital opening. This pair of spines may be considered to be homologous with the parallel sclerites which are typical for Section 5 (van Hille, 1984). Parallel to the distal half of these spines but not extending as far distally, is a pair of shorter spines with narrow base and pointed apex; distally to the apex of these spines lie three parallel spines on each side; distally to these is a pair of very short spines lying close together in the median area. A longitudinal strand runs from the base of the basal cap distally to beyond the genital opening; a similar strand was seen in *A.* (*A.*) *vandersteli* (van Hille, 1985b) where it was thought to be attached to the base of the most distal spine; less distinct this structure was seen in *A.* (*A.*) *sebastiani* (van Hille, 1985a). Spiculum gastrale (Fig. 7) asymmetrical. Last exposed abdominal sternum with flattened apex.

MATERIAL EXAMINED. South Africa: Namaqualand Coast, Buffelsrivier, 29° 55′S, 17° 40′E, 28.viii.1977, 1347, groundtraps, millipede bait, 59 days, Holotype ♂, Paratypes 1♂, 3♀♀, (S. Endrödy-Younga); Richtersveld, Buffelsriv[ier] Valley, 29° 35′S, 17° 27′E, 31.viii.1976, 1193, groundtraps, banana bait, 35 days, Paratypes 1♂, 2♀♀, (S. Endrödy-Younga). The Holotype and 5 Paratypes (2♂♂, 3♀♀) are in the Transvaal Museum; 2 Paratypes (♀♀) are in the Albany Museum, Grahamstown.

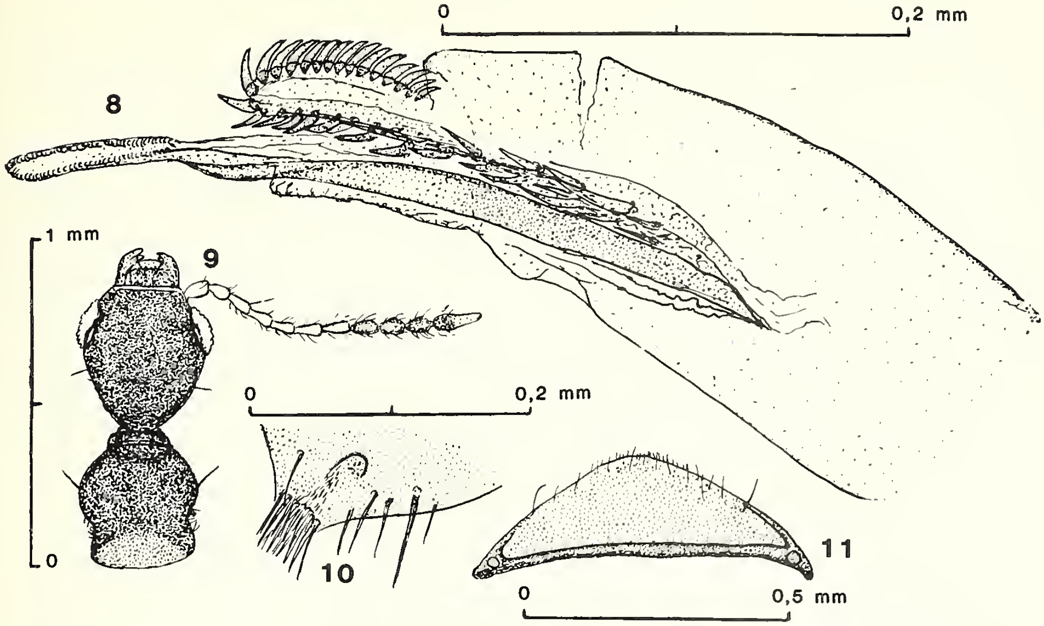
This species belongs in the specialised group of species in Section 5, with *A.* (*A.*) *apterus* and *A.* (*A.*) *halleyi* (see above). It comes nearest to *A.* (*A.*) *vandersteli* (van Hille, 1985b) which, however, has the peculiarity of unpaired spines in the connecting membrane of the aedeagus.

SECTION 6

Anthicus (Aulacoderus) propinquus **spec. nov., Figs 8–11**

Size. Length 2,41 mm (2,15–2,72); width over broadest part of elytra 0,39 mm (0,74–1,17).

Head (Fig. 9). Glossy; very dark testaceous to black; longitudinally oval. Punctures dorsally



Figs. 8–11. *A.* (*A.*) *propinquus* spec. nov. 8: aedeagus. 9: head and prothorax. 10: apex of elytron of male. 11: last exposed abdominal sternum.

fine, ventrally bigger but absent in median ventral area; with fine procumbent hairs and with a few longer semi-erect dark hairs laterally and dorsally. Eyes on anterior half of head, with dark margin and bulging.

Prothorax (Fig. 9). Glossy: black; longer than broad, narrower than head. Shoulders sloping and rounded. Lateral constrictions at posterior third, with fine hairs. Punctures more distinct than on head, dorsally surrounded by a small dark area, absent on posterior third; ventrally bigger than dorsally with fine recumbent hairs and a pair of long dark lateral hairs.

Elytra. Glossy; black; greatest breadth in front of middle. Punctures more widely spaced than on prothorax, with fine recumbent hairs, slightly longer than on prothorax. In male (Fig. 10) with elongate notch and an apical tuft of about 20 short spiny hairs.

Wings. Fully developed.

Antennae (Fig. 9). Slender; light testaceous, apical four segments darker but apical half of last segment light testaceous.

Legs. Testaceous; coxae, femora and proximal part of tibiae somewhat darker to almost black; tarsi lighter.

Undersurface. Testaceous to dark testaceous to almost black with mesepimerite apophyses but spiral markings indistinct.

Male abdomen: Aedeagus (Fig. 8): tegmen little sclerotised, apical piece about 1/3 of the length of basal piece; median lobe slender with elongate apical genital opening with finely beaded margin; connecting membrane with single dorsal row of about 24 spiny teeth but in the region where the connecting membrane is attached to the base of the median lobe, the spines are

larger and are not strictly aligned in a single row. Last exposed abdominal sternum (Fig. 11) with dark basal margin and rounded apex with a fringe of short hairs.

MATERIAL EXAMINED. South Africa: Zululand, Eshowe [2831CD], 19.xii.1985, on climbers and branches inside Gunze Forest, Holotype ♂, Paratypes 9 ♀♀, (P. E. Reavell). The material is in the Albany Museum, Grahamstown.

This species comes very close to *A.* (*A.*) *convexus* Pic, 1903 (van Hille, 1984, Figs 181–186). The aedeagi of the two species are similar, both have the elongate head and prothorax and the two-coloured apical antennal segment. However, *A.* (*A.*) *propinquus* is longer than *A.* (*A.*) *convexus* and the sizes do not overlap; also *A.* (*A.*) *propinquus* is darker. But both size and colour are variable within the species. The prothorax of *A.* (*A.*) *propinquus* is more elongated than of *A.* (*A.*) *convexus*. The apex of each elytron of the male of *A.* (*A.*) *convexus* has a stout dark spine at the median side of the notch and a row of about six short thick hairs at the lateral side of the notch. *A.* (*A.*) *propinquus* has a tuft of spiny hairs which fills the notch. The fringe of short hairs on the apex of the last exposed abdominal sternum of the male is continuous in *A.* (*A.*) *propinquus*; in *A.* (*A.*) *convexus* it is interrupted in the middle. *A.* (*A.*) *convexus* was collected in Eshowe in 1926 by R. E. Turner, but it does not occur in the recent collections of P. E. Reavell.

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Prey selection in several sympatric species of *Ammophila* W. Kirby (Hymenoptera: Sphecidae) in southern Africa*

by

A. J. S. WEAVING

(Albany Museum, Grahamstown)

ABSTRACT

Prey selection by several sympatric species of *Ammophila* W. Kirby was investigated. Prey-size requirements differed according to the size of wasps and their provisioning strategies but, because of overlap and changes in caterpillar size during development, this did not wholly explain observed interspecific differences in species and families of caterpillars taken. Differences were mainly the result of wasps hunting in different types of vegetation in which the most abundant, suitably-sized caterpillars were taken. Specialisation by individuals on certain prey species indicated locality learning, maximising prey utilisation. The possibility of the observed prey selection being due to competition is discussed.

INTRODUCTION

All aculeate wasps, with the exception of most species of Masaridae, feed in the larval stage on insects or spiders. Adults are predatory in that they hunt to provide for their offspring, although generally they themselves feed mainly on nectar. Most aculeate wasp families are more or less prey specific, usually at the ordinal level, but radiation within the Sphecidae has produced forms which exploit adult and immature insects from most orders as well as springtails and spiders (Evans, 1966). Within this family, however, prey specificity may extend even to the specific level and can act as a taxonomic character (Evans, 1966).

Selection of prey by individual wasp species, and amongst closely related species, has been reported by many workers. Studies in which prey populations themselves have been investigated as well demonstrate that prey selection is often related to the size of predator and prey, the availability and behaviour of the prey, flexibility in predatory behaviour, and particularly the preferred hunting habitat of the predator (Bowden, 1964; Coville, 1976; Evans, 1953 and 1966; Gwynne, 1979 and 1981; Kurczewski and Kurczewski, 1968; Laing, 1979; McQueen, 1979; Muma and Jeffers, 1945; O'Brien, 1982; O'Neill and Evans, 1982 and Rau, 1935). The existence of distinct prey preferences, particularly amongst closely related species occurring sympatrically, might also be interpreted as being the outcome of interspecific competition (O'Neill and Evans, 1982). While it is obvious that the potential for competition is reduced as a result of preferences

*From a dissertation approved for the degree of Master of Science, Rhodes University.

for different prey and hunting environments (Evans, 1959), no one has demonstrated that the development of these preferences has actually been brought about by competition.

Digger wasps of the genus *Ammophila* hunt for lepidopterous, sometimes hymenopterous, caterpillars (Bohart and Menke, 1976) which occur amongst foliage during the day (Powell, 1964). Different species are reported to select caterpillars mainly on the basis of size, availability and habitat (Evans, 1959 and 1965; Powell, 1964), but no detailed interspecific comparison has been published for a group of sympatric species. The existence of several species nesting at one locality in the Eastern Cape has provided an opportunity to investigate prey selection among species of *Ammophila* exposed to the same population of caterpillars and to identify the factors governing any observed choice of prey.

The species investigated in the present study were *Ammophila beniniensis* (Palisot de Beauvois), *A. braunsi* (Turner), *A. conifera* (Arnold), *A. dolichocephala* Cameron, *A. dolichodera* Kohl, *A. ferrugineipes* Lepeletier, *A. insignis* F. Smith and *A. vulcania* du Buysson.

Direct interspecific comparisons of prey selection were made on the farm Hilton, 18 km WNW of Grahamstown in the Eastern Cape Province of South Africa (33°19′S, 26°32′E). A full description of the site is given by Gess (1981). Supplementary data were obtained from the farms Clifton (33°11′S, 26°24′E), also near Grahamstown, and Verdun (33°09′S, 25°51′E) near Kommadagga, and in Natal from Mkuze Game Reserve (27°40′S, 32°08′E), Hluhluwe Game Reserve (28°07′S, 32°03′E) and Fanies Island (28°03′S, 32°26′E) by Lake St Lucia.

METHODS

Determination of prey preferences

Samples of the prey of *Ammophila* were obtained by opening as many recently provisioned nests as possible. Supplementary records were provided by wasps found transporting their prey. The size and mass of all prey were recorded for investigating size preferences shown by the wasps.

The prey caterpillars could not of course be reared to the adult stage for identification, having been permanently paralysed by the wasps. Instead, caterpillars occurring on dominant plant species at the site were sampled over two years. This also served to indicate major seasonal fluctuations in their availability. Samples of each type of caterpillar were coded, photographed in colour and reared to the adult stage for identification. Wherever necessary, notes or sketches were made of distinguishing features. The maximum size and mass attained by each species prior to pupation was also recorded. Caterpillars from wasps' nests were identified by comparison with coded larvae being reared or, if these were not available at the time, with the colour photographs.

The plants sampled were the six most common trees/shrubs, *Acacia karroo* (Leguminosae), *Diospyros dichrophylla* (Ebenaceae), *Rhus macowanii* (Anacardiaceae), *Maytenus linearis*, *M. heterophylla* (Celastraceae) and *Lycium campanulatum* (Solanaceae), and the very abundant dwarf shrub *Chrysocoma tenuifolia* (Compositae). Trees and shrubs were sampled by beating selected branches with a stout stick over a cloth-covered beating tray of 0,36 m^2. Sampling was standardised by following a procedure similar to that used by White (1975). The selected branch was given four sharp taps, this being repeated three more times using different branches which had not been disturbed by the previous sampling, not necessarily on the same shrub or tree. The resulting sample made up one replicate, ten of which were taken from each plant species on each sampling occasion, usually every two

weeks. The dwarf shrub was not amenable to the beating technique and instead 40 randomly selected plants were searched for caterpillars.

RESULTS

Prey taxon

The frequencies with which lepidopterous families were represented in the prey used by different species of *Ammophila* are given in Table 1. The use of caterpillars from different families differed significantly between the three most abundant *Ammophila* species. Chi-squared values for the species comparisons *A. dolichodera*/*A. ferrugineipes*, *A. insignis*/*A. ferrugineipes* and *A. dolichodera*/*A. insignis* were 151,30 (df = 5), 123,48 (df = 3) and 135,13 (df = 3) respectively, significant at levels well below p = 0,001. Differences in prey family utilisation are also evident for the five inadequately sampled species for which data are presented qualitatively.

TABLE 1

Prey usage by *Ammophila* at Hilton according to families of Lepidoptera.

Species of *Ammophila*	n	Arc	Las	Noc	Geo	Lyc	Pie	Pyr
		Per cent of prey attributable to family						
A. dolichodera	34	26,4	52,9	17,6	0,0	0,0	0,0	0,0
A. insignis	138	0,0	0,0	64,3	35,4	0,0	0,0	0,0
A. ferrugineipes	125	0,0	0,0	1,6	81,0	15,9	0,8	0,0
A. beniniensis	3	–	–	+	–	–	–	–
A. vulcania	8	–	–	+	–	–	–	–
A. braunsi	7	–	–	+	–	–	–	–
A. dolichocephala	12	–	–	+	+	–	–	–
A. conifera	3	–	–	–	–	+	–	+

Abbreviations: Arc = Arctiidae, Las = Lasiocampidae, Noc = Noctuidae, Geo = Geometridae, Lyc = Lycaenidae, Pie = Pieridae, Pyr = Pyralidae.

A. dolichodera was the only species that took hairy arctiid and lasiocampid caterpillars. These accounted for almost 80 per cent of its prey. The remainder consisted of smooth, noctuid caterpillars. Noctuidae were taken by all the species of *Ammophila* except *A. conifera*, and were the most common prey of *A. insignis*. Nests of *A. braunsi*, *A. beniniensis* and *A. vulcania* were stocked exclusively with Noctuidae. Prey of *A. ferrugineipes* consisted mostly of geometrid caterpillars (81 per cent) and only occasional noctuid caterpillars (1,6 per cent). Lycaenidae were included in the prey of both *A. ferrugineipes* and *A. conifera*, the latter also taking Pyralidae.

The species of prey taken are given in Table 2 which shows that only six out of a total of 42 species of caterpillars were shared between any of the *Ammophila* species. Calculated niche overlaps for this resource (Table 3) are consequently very low for all species pairs comparisons. Supplementary data obtained from a site in Mkuze Game Reserve over a ten-day period showed no overlap whatever in prey taken by *A. ferrugineipes* and *A. beniniensis*. Nests of the latter species (n = 7) were stocked with caterpillars of the noctuid *Achaea lienardi*, those of the former species (n = 27) with geometrid caterpillars (7) or with noctuid caterpillars of the subfamily Plusiinae (20). In this area noctuid caterpillars formed the main prey of *A. ferrugineipes*, in contrast to what was found at Hilton (Table 1). Thus, whereas the type of prey taken varied between sites a lack of interspecific overlap persisted.

TABLE 2

Caterpillar species taken as prey by *Ammophila* at Hilton.

Species of *Ammophila*	Prey species	Species of *Ammophila*
	ARCTIIDAE	
dolichodera	*Maenas vocula*	
	LASIOCAMPIDAE	
dolichodera	*Beralade prompta*	
dolichodera	*Pachypasa* sp.	
dolichodera	*Bombycopsis nigrovittata*	
	NOCTUIDAE	
dolichodera	indet. catocaline	
	Heliothis armigera	*braunsi*
	Craterestra definiens	*braunsi*
dolichodera	*Cucullia minuta*	*dolichocephala*
insignis	*C. consimilis*	
dolichodera, *insignis*	Noct. Z	
insignis	*Blenina squamifera*	
insignis	*Anua selenaris*	
insignis	*Eutelia adulatrix*	
insignis	*Hypoplexia externa*	
insignis	Noct. I	
insignis	*Ulotrichopus primulina*	
insignis, *ferrrugineipes*	*Audea melaleuca*	
insignis	Noct. 3	
insignis	? *Achaea* sp. (Noct. J)	*beniniensis*
	Thria robusta	*beniniensis*
	indet. noctuid	*beniniensis*
	? *Achaea* sp.	*vulcania*
	GEOMETRIDAE	
insignis	*Axiodes bifasciata*	*dolichocephala*
	A. dochmoleuca	*dolichocephala*
insignis	*Omphalucha ditriba*	
insignis	Geom. D	
insignis, *ferrrugineipes*	Geom. F	
ferrrugineipes	*Syndromodes invenusta*	
ferrrugineipes	*Tephrina* / *Semiothisa* spp.	
ferrrugineipes	*Zamarada* spp.	
ferrrugineipes	*Ligdia pectinicornis*	
ferrrugineipes	*Lomographa indularia*	
ferrrugineipes	*Prasinocyma scissaria*	
ferrrugineipes	Geom. J/X	
ferrrugineipes	Geom. 19+28+30	
	LYCAENIDAE	
ferrrugineipes	*Anthene* spp.	*conifera*
	PIERIDAE	
ferrrugineipes	*Pieris helice*	
	PYRALIDAE	
	indet. pyralid	*conifera*

Broken line linking wasp species with prey indicates record from Clifton.

Table 3

Niche overlaps for three species of *Ammophila* at Hilton.

Resource set	*Niche overlaps* for respective species pairs* *dolichodera/ insignis*	*dolichodera/ ferrugineipes*	*insignis/ ferrugineipes*
Prey length	0,559	0,062	0,547
Prey mass	0,146	0,000	0,204
Prey species	0,018	0,000	0,012
Hunting habitat (plant species)	0,099	0,843	0,118
Hunting habitat (generalised)	0,721	0,757	0,238

*Calculated using symmetric MacArthur-Levins formula (Lawlor, 1980).

Size of prey

Sizes of prey differed markedly between the various species of *Ammophila*. The mass and length of caterpillars sampled from nests are given in Table 4, grouped according to whether the wasps provision their nests with one or several prey (Weaving, in press). As would be expected, single-prey species on average selected much larger caterpillars than did the multiple-prey species. Further size differences occurred within each group, showing a positive correlation between prey size and wasp size. However, interspecific overlap in prey size, particularly with regard to prey length, was extensive (Fig. 1 and Table 3) due to the wide range in prey size taken by each species. The potential for interspecific competition for prey on the basis of size therefore exists for most of the species. The niche overlap value of 0,559 between the single-prey species *A. dolichodera* and multiple-prey species *A. insignis* can be explained on their size difference, the substantially larger size of the latter species counteracting its requirement for smaller prey dictated by its provisioning strategy. *A. dolichodera* is similar in size to the multiple-prey species *A. ferrugineipes* and in this case the overlap value is very low (0,062) due to their differing provisioning strategies.

Niche overlap values were not calculated for the remaining species because of the small sample sizes. Nevertheless, the data in Fig. 1 and Table 4 show that prey taken by the two single-prey species *A. beniniensis* and *A. braunsi* fall entirely within the size range of that taken by *A. dolichodera*. A similar relationship occurs between the multiple-prey species *A. conifera*, *A. dolichocephala* and *A. ferrugineipes*. Only *A. vulcania* in the Eastern Cape selected prey entirely outside the range of sizes for all of the other species.

An intraspecific comparison of data for *A. ferrugineipes* from Hilton and the Natal sites confirms that, apart from provisioning strategy, the size of the wasp governs the size of prey taken. Caterpillars taken in Natal were significantly longer than those at Hilton (mean length = 20,6 and 15,9 mm respectively, Student's $t = 2{,}866$ $df = 26$ $p < 0{,}01$). Wasp size was also significantly greater in Natal (mean head width = 3,81 and 3,41 mm respectively, Student's $t = 5{,}228$ $df = 29$ $p < 0{,}001$). However, there was no significant difference between sites in the ratios of wasp size to prey length (ratio = 0,460 and 0,403 respectively, Student's $t = 1{,}417$ $df = 26$ $p > 0{,}1$). This species was therefore taking larger caterpillars in Natal simply because of its larger size.

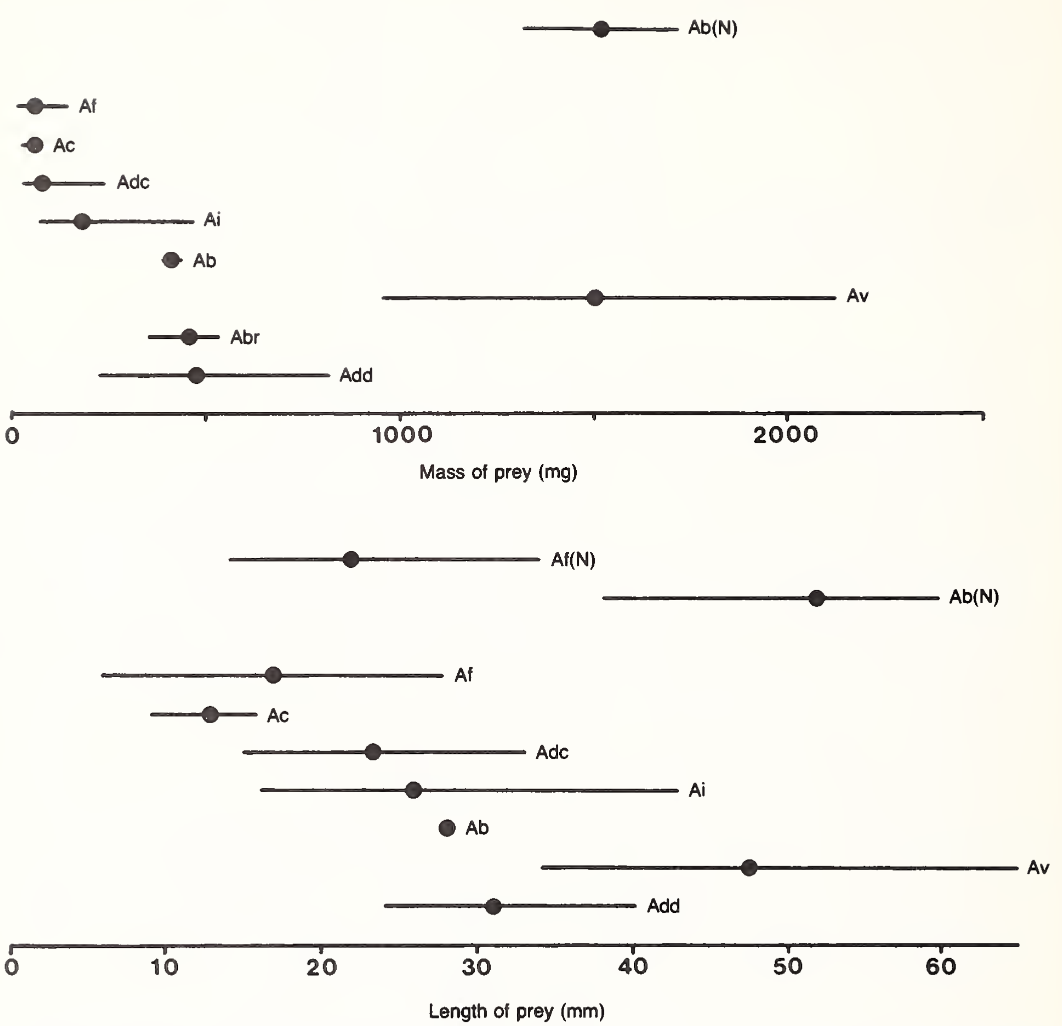


Fig. 1. Mean mass/length (●) of prey and range (————) taken by various species of *Ammophila* at Hilton, and in Natal (N) as indicated. Ab — *Ammophila beniniensis;* Abr — *A. braunsi;* Ac — *A. conifera;* Adc — *A. dolichocephala;* Add — *A. dolichodera;* Af — *A. ferrugineipes;* Ai — *A. insignis;* Av — *A. vulcania.*

Table 4.

Sizes of prey used by eight species of *Ammophila* at Eastern Cape sites except when otherwise indicated.

Species of *Ammophila*	Wasp length* mm	Wasp mass# mg	*Mean size of prey* mass mg	n	length mm	n	Mass of prey / Mass of wasp	y
Single-prey species:								
braunsi	20	53	439	7	27	3	9,4(5,7–12,5)	4
dolichodera	23	72	466	26	31	29	8,5(4,4–13,3)	5
beniniensis	24	48	408	2	28	2	9,1	1
beniniensis Natal	31	169	1515	2	52	22	9,4(6,7–12,1)	2
vulcania	31	273	1503	7	48	7	3,8(3,0–7,1)	4
Multiple-prey species:								
conifera	22	53	40	3	17	6	0,3	1
ferrugineipes	22	52	52	106	17	105	1,3(0,7–2,3)	19
dolichocephala	27	108	85	11	21	11	0,6(0,2–2,1)	8
insignis	30	122	185	107	26	126	1,0(0,7–1,7)	6

*Mean of 10 specimens. # Mean of variable number of specimens of each species. y Number of direct prey mass/wasp mass comparisons.
Ranges in parentheses.

Source of prey

The proportions of prey originating from various plant species are shown in Fig. 2 for three well-sampled species of *Ammophila*. Twenty-three per cent of the prey of *A. insignis* originated from *Diospyros dichrophylla* and *Rhus macowanii*, trees and large shrubs confined to the banks of the watercourses. *Acacia karroo*, which accounted for a further six per cent, occurred in various growth forms, large trees along the watercourses and elsewhere, smaller trees and shrubs, and low shrubs less than a metre high. A similar proportion (five per cent) came from *Lycium campanulatum*, small to medium sized shrubs scattered over the area. Thirty-nine per cent of prey was obtained from *Pentzia incana* (Compositae), a component of the low-growing dwarf karroid scrub, and the remaining 27 per cent from unknown sources. Disregarding the unknown sources, a significant proportion of the prey of *A. insignis* (32 per cent) therefore originated from trees and large shrubs and this could be as high as 40 per cent if caterpillars from *A. karroo* came from trees of this species growing along the watercourses. However, the origin of 60 per cent of prey from *L. campanulatum* and *P. incana* shows that *A. insignis* was flexible in its hunting habitat. Nevertheless, it is the only one of the three well-sampled species, *A. ferrugineipes*, *A. insignis* and *A. dolichodera*, which obtained some of its prey from *R. macowanii*, *D. dicrophylla* and *L. campanulatum*.

More than 90 per cent of the prey of *A. ferrugineipes* was from *A. karroo*, and the few direct observations of this species catching its prey involved moderate-sized shrubs away from the watercourses. At Hilton less than one per cent originated from low-growing plants. In Natal *A. ferrugineipes* took prey from herbaceous plants too and it is therefore another species showing versatility in its choice of hunting habitat.

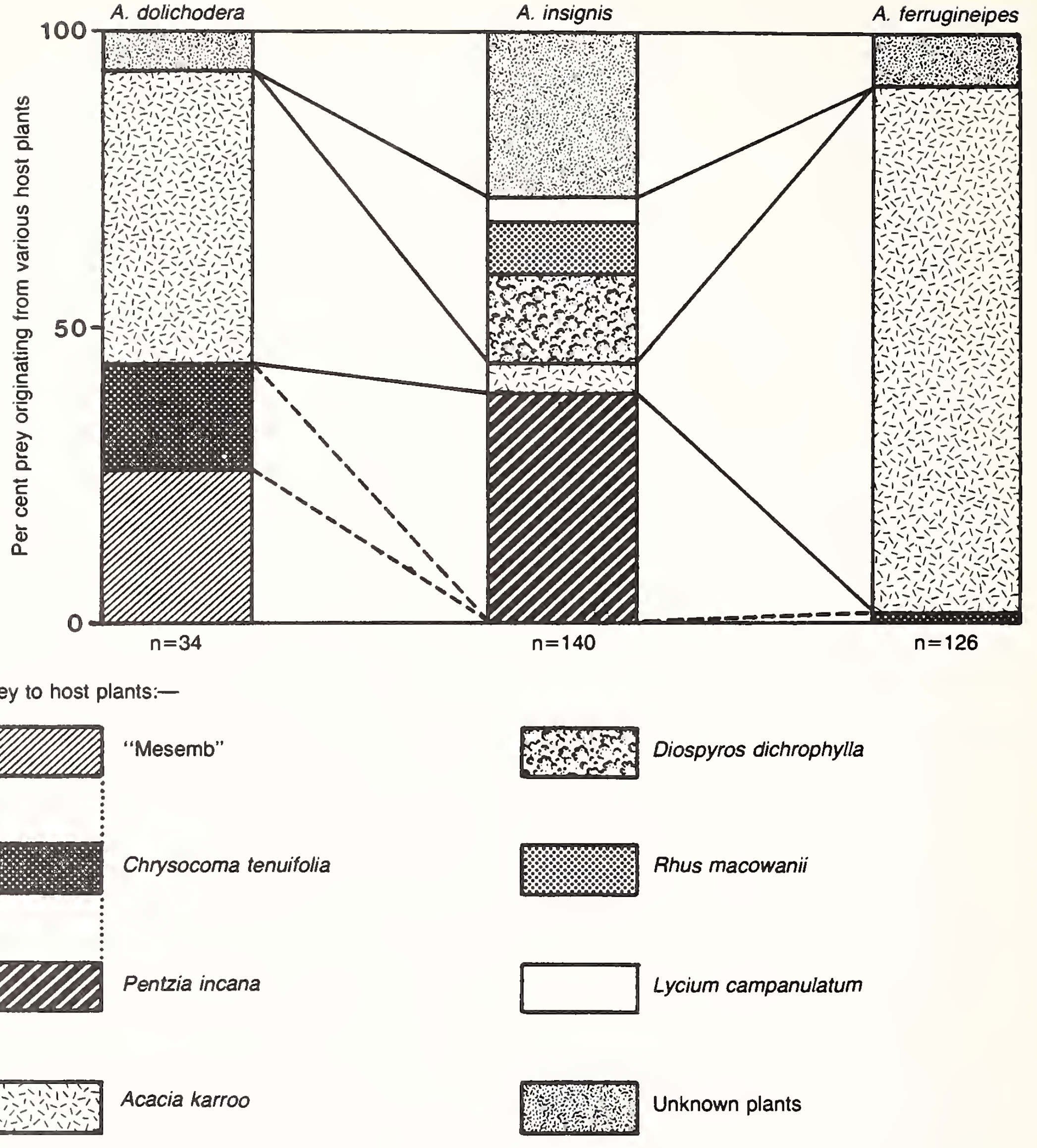


Fig. 2. Sources of caterpillar prey taken by three species of *Ammophila* at Hilton. Plants linked by dotted lines in the key are dwarf shrubs. *Lycium campanulatum* is a shrub. *Rhus macowanii*, *Diospyros dichrophylla* and *Acacia karroo* occur as trees mainly along watercourses, the last two species also as smaller trees and small shrubs elsewhere.

A. dolichodera obtained 44 per cent of its prey from dwarf shrubs and 50 per cent from *A. karroo*. A high niche overlap value of 0,843 (Table 3) shows that much of the prey of this species and of *A. ferrugineipes* is obtained from the same plant species; interestingly, the same species pair showed no overlap in species of caterpillars selected. In reality, however, the overlap in hunting habitat is probably much less. *A. dolichodera* was always observed hunting in the smallest of the three size categories of *A. karroo* mentioned above and therefore probably obtains its prey from low-growing vegetation only.

The origins of the prey of the remaining species of *Ammophila*, for which sample sizes are very small, are indicated in Table 5. *A. braunsi* hunts in low-growing vegetation, utilising the same type of vegetation as does *A. dolichodera*. However, the former species' preference for areas of clay soil (Weaving, 1986) effectively separates the hunting habitats of both species. The hunting habitat of *A. dolichocephala*, the only multiple-prey species which hunted in low-growing vegetation, overlapped with that of both the above species since it was recorded from sand and clay areas (Weaving, 1986).

TABLE 5

Sources of prey of five poorly sampled species of *Ammophila* at various localities.

Species and locality	Source of prey
A. braunsi	
Hilton (n = 6)	*Atriplex semibaccata*[a]—low-growing herb
Kommadagga (n = 1)	*Atriplex semibaccata*[a]—low-growing herb
A. beniniensis	
Hilton (n = 3)	One unknown, others below leaf litter
A. vulcania	
Hilton (n = 3)	Unknown—suspected *Rhus macowanii*
Clifton (n = 5)	*Pappea capensis*[b]— small trees in dwarf karroid scrub
A. conifera	
Hilton (n = 3)	*Acacia karroo* and, probably, *Maytenus* spp.
A. dolichocephala	
Hilton (n = 7)	*Chrysocoma tenuifolia*— dwarf shrub <0,5 m high
Clifton (n = 3)	*Pentzia incana*—dwarf shrub <0,5 m high

[a]—Chenopodiaceae; [b]—Sapindaceae.

At Hilton there were two instances of *A. beniniensis* obtaining its prey from below leaf litter, behaviour which has not previously been documented for *Ammophila*. In Natal this species hunted in large trees. The hunting habitat of *A. vulcania* in the Eastern Cape was similar to that of *A. beniniensis* in Natal in spite of the difference in the general habitat (Weaving, 1986).

A comparison between ranges in the size of prey taken by *A. ferrugineipes*, *A. insignis* and *A. dolichodera* and the maximum sizes attained by prey species and potential prey species reared in the laboratory (Figs 3 and 4) provides further evidence of the hunting habitats used. Relative abundance of the various caterpillar species, as determined by field collections, is shown in Appendix I. Caterpillars of Geom 6 (abundance rating AR = 1), *Xylopteryx arcuata* (AR = 7) and *X. prasinaria* (AR = 8) attained suitable sizes and were more abundant than most of the species utilised as prey. Their absence from nests of *A. ferrugineipes* confirms that this species does not hunt in *D. dichrophylla*, *R. macowanii* or *Maytenus* spp.

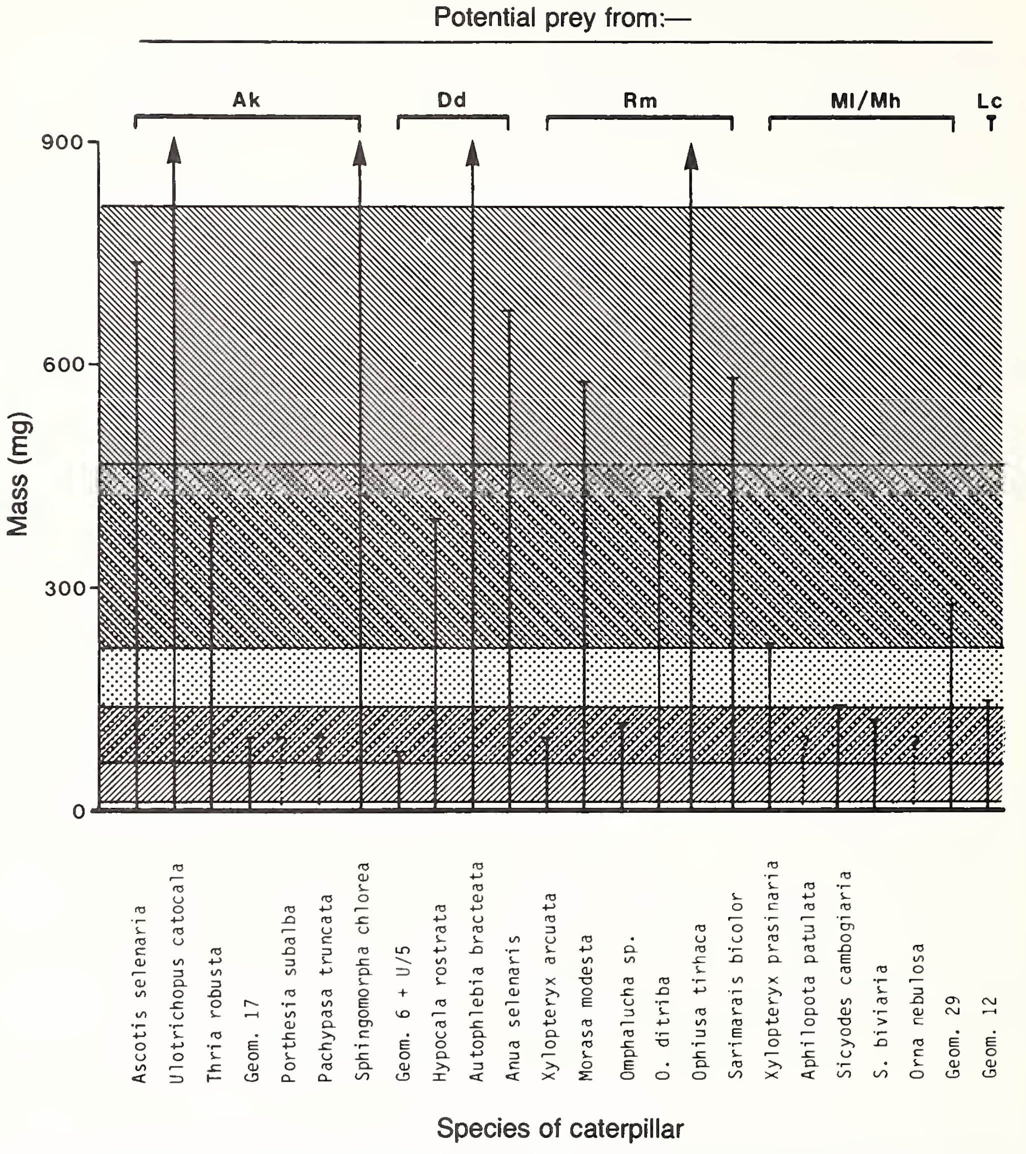
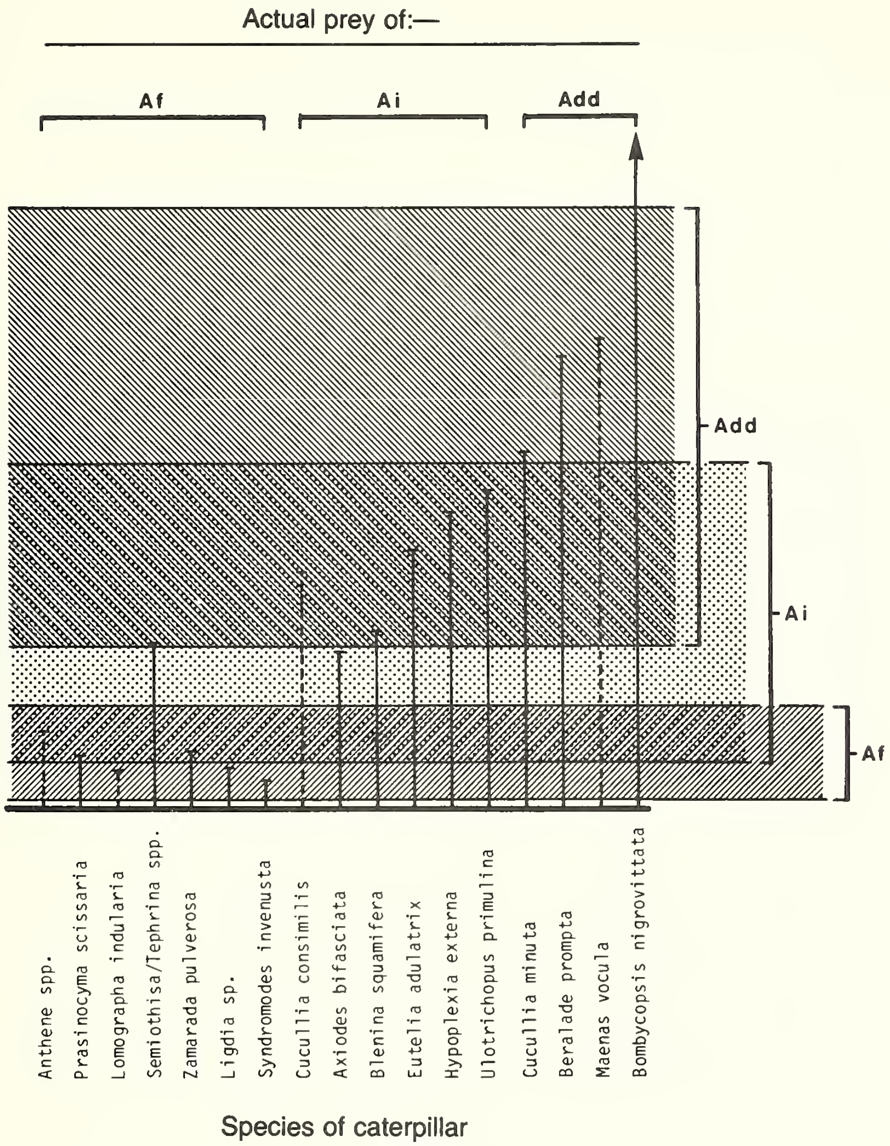


Fig. 3. Ranges in the mass of caterpillars of actual and potential prey species (vertical bars) at Hilton, and limits of mass of individual prey (horizontal shaded bands) taken by three species of *Ammophila*. Add — *A. dolichodera;* Af — *A. ferrugineipes;* Ai — *A. insignis*. Ak — *Acacia karroo;* Dd — *Diospyros dichrophylla;* Ly — *Lycium campanulatum;* Mh — *Maytenus heterophylla;* Ml — *M. linearis;* Rm — *Rhus macowanii.*


Actual prey of:—
Af
Ai
Add
Add
Ai
Af
Anthene spp.
Prasinocyma scissaria
Lomographa indularia
Semiothisa/Tephrina spp.
Zamarada pulverosa
Ligdia sp.
Syndromodes invenusta
Cucullia consimilis
Axiodes bifasciata
Blenina squamifera
Eutelia adulatrix
Hypoplexia externa
Ulotrichopus primulina
Cucullia minuta
Beralade prompta
Maenas vocula
Bombycopsis nigrovittata
Species of caterpillar

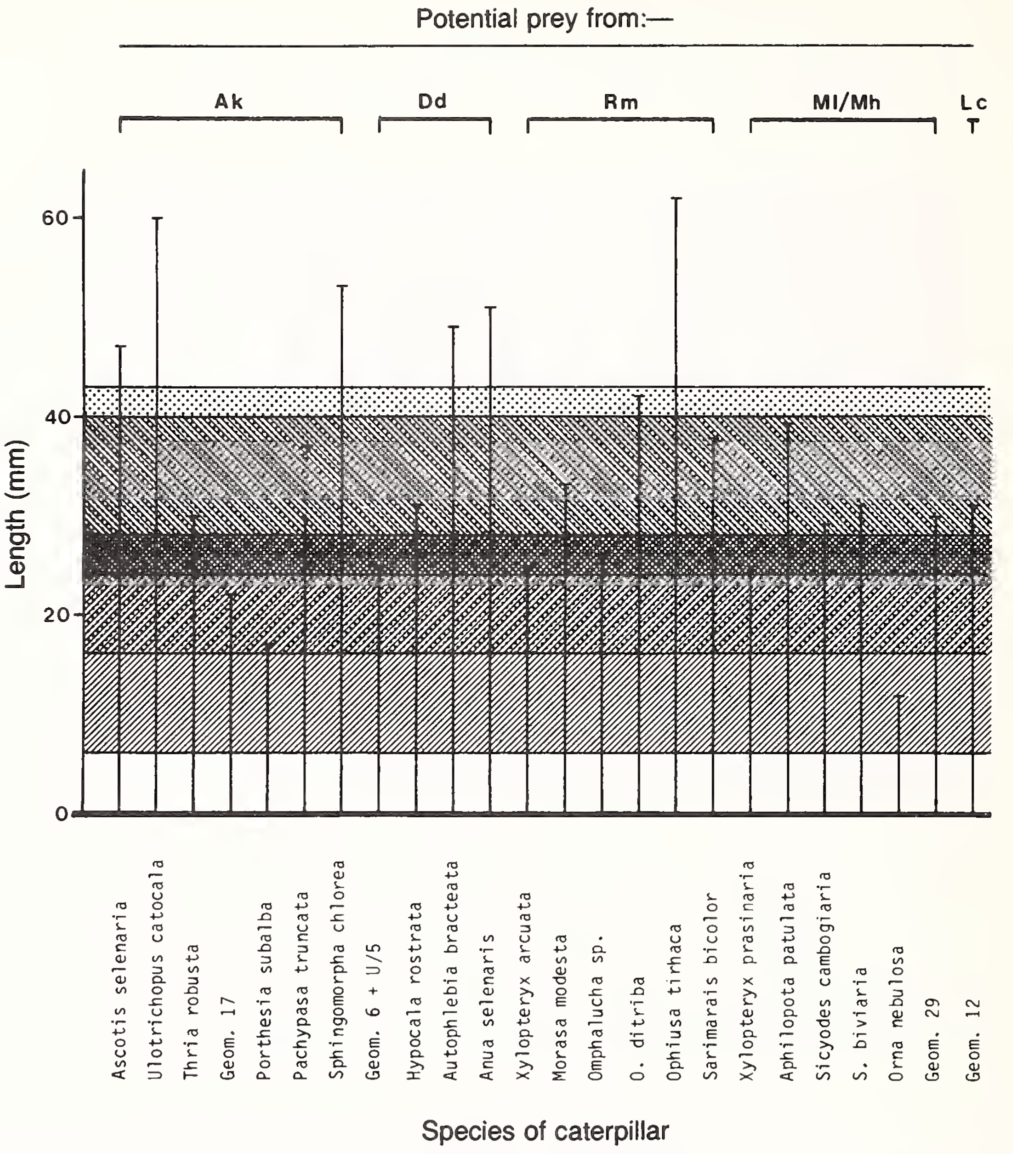
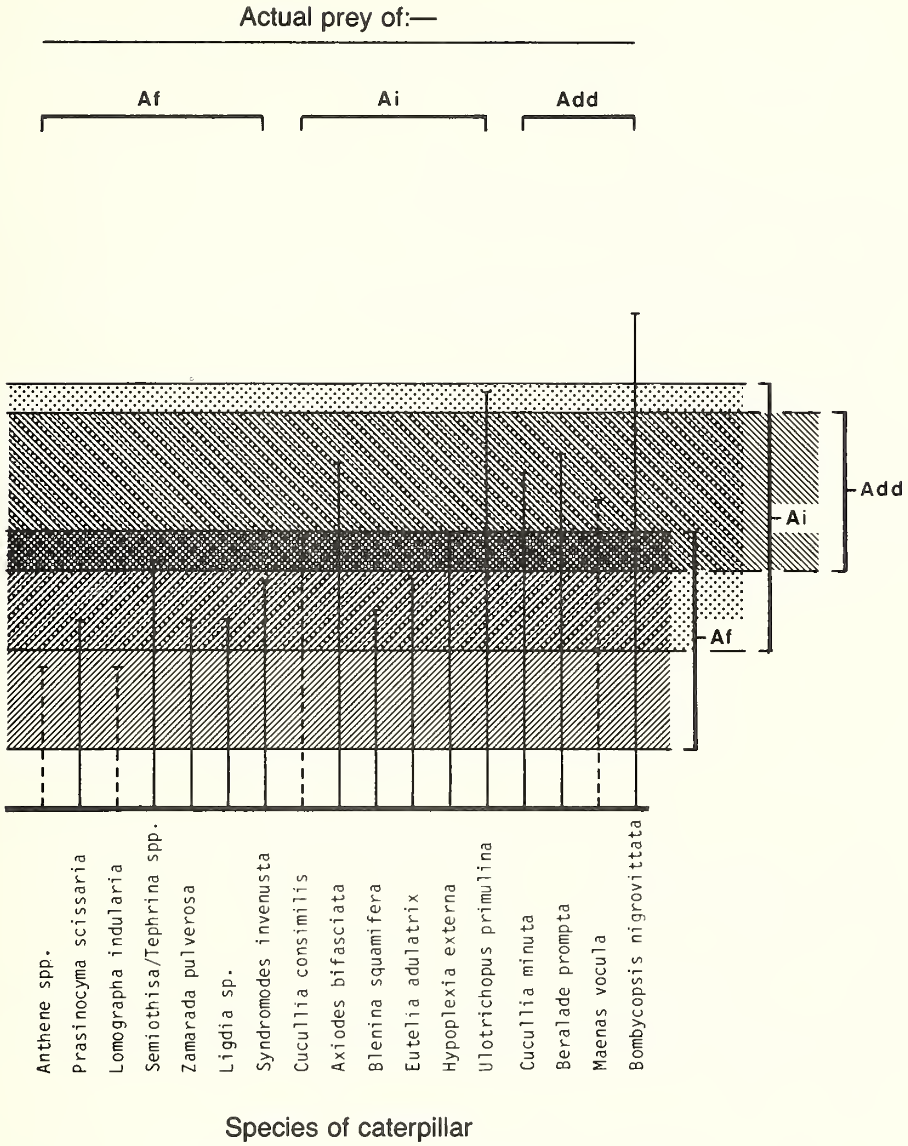


Fig. 4. Ranges in the length of caterpillars of actual and potential prey species (vertical bars) at Hilton, and limits of length of prey (horizontal shaded bands) taken by three species of *Ammophila*. Abbreviations as in Fig. 3.


Actual prey of:—
Af
Ai
Add
Add
Ai
Af
Anthene spp.
Prasinocyma scissaria
Lomographa indularia
Semiothisa/Tephrina spp.
Zamarada pulverosa
Ligdia sp.
Syndromodes invenusta
Cucullia consimilis
Axiodes bifasciata
Blenina squamifera
Eutelia adulatrix
Hypoplexia externa
Ulotrichopus primulina
Cucullia minuta
Beralade prompta
Maenas vocula
Bombycopsis nigrovittata
Species of caterpillar

During a period when the noctuid *Cucullia minuta* was extremely abundant on *Chrysocoma tenuifolia*, it was not taken by *A. ferrugineipes* even though earlier instars would have been suitably sized. The geometrid *Axiodes dochmoleuca* also occurred on this plant and was taken by *A. dolichocephala*; although of a suitable size, it was never recorded as prey of *A. ferrugineipes*. These observations confirm what has been stated above concerning the different hunting habitats of these two species.

Morasa modesta, a hairy lymantriid caterpillar found on *R. macowanii* (AR = 17) was suitably sized for *A. dolichodera* but never taken by it. This supports the observation that *A. dolichodera* hunts only in low-growing vegetation.

A. insignis obtained 16 per cent of its prey from *D. dichrophylla* (Fig. 2). However, in spite of its abundance on this plant, Geom 6 (AR = 1) was never recorded as prey. Although mature caterpillars reached a suitable length (Fig. 4), their maximum mass only slightly exceeded the minimum recorded for *A. insignis*. Many specimens would probably be smaller and would thus be rejected, which may explain their absence from nests of *A. insignis*. The caterpillars of a sawfly, *Arge* sp. (Hymenoptera, Argidae) (AR = 9) occurred on the same plant. Mature specimens reached 25 mm in length and, as indicated by their diameter of 4 mm, were similar in mass to caterpillars of a noctuid *Blenina squamifera* which were frequently taken as prey from *D. dichrophylla*. It is of interest that caterpillars of *Arge* sp. were never taken by *A. insignis* since sawfly caterpillars have been recorded elsewhere as prey of *Ammophila* (Bohart and Menke, 1976).

The above observations are summarised in Table 6 in which the various species of *Ammophila* at Hilton have been allocated to one of four categories of vegetation/hunting habitat. From this it is evident that there is potential competition for prey between several species as a result of hunting in the same habitats, especially as it has already been shown that prey size requirements overlap extensively.

TABLE 6

Distribution of species of *Ammophila* between four categories of hunting habitat at Hilton with supplementary information from other localities.

Hunting habitat	*Occurrence of respective species of Ammophila*						
	Single-prey species				*Multiple-prey species*		
	Ab	Abr	Add	Av	Adc	Af	Ai
Shrubs and trees bordering watercourses	—	—	—	+[a]	—	—	+
Shrubs and trees away from watercourses	—	—	—	+[b]	—	+	+
Low-growing vegetation	—	+[c]	+[d]	—	+[e]	—	+
Leaf litter below shrubs and trees	+[f]	—	—	—	—	—	—

Abbreviations: Ab — *A. beniniensis*; Abr — *A. braunsi*; Add —*A. dolichodera*; Av — *A. vulcania*; Adc — *A. dolichocephala*; Af —*A. ferrugineipes*; Ai — *A. insignis*.

[a]—suspected; [b]—observations at Clifton; [c]—confirmed by observations at Verdun; [d]—confirmed by observations at Mkuze Game Reserve; [e]—confirmed by observations at Clifton; [f]—all Natal records involved hunting in large trees in well-vegetated areas.

Another aspect of the source of prey, for which there is very little information, is the position that the prey occupies on the host plant. Observations of caterpillars in the field and of those being reared have indicated which species are to be found amongst foliage and those which spend the day either resting along branches or below leaf litter. The most frequently taken prey of *A. ferrugineipes* for which observations were available were mostly green, foliage-inhabiting

forms. *A. insignis* included both foliage-inhabiting species and those found on branches. The form of dwarf shrubs makes it difficult to draw this distinction, but the prey of *A. dolichodera* from *A. karroo*, the lasiocampids *Beralade prompta*, *Pachypasa* sp. and probably the unidentified catocaline noctuid, were branch inhabiting forms during the day. Such differences help to explain the almost complete absence of shared prey species even among *Ammophila* which hunt in the same plant types, but further data are essential before any firm conclusions can be drawn.

Relative abundance and seasonality of prey

The seasonal distribution of records of the more abundant caterpillar species, including those obtained from sampling wasps' nests, are shown in Table 7. All species were present for at least half of the period when *Ammophila* were active (October to May) and many of them for all or most of it. Since both *A. ferrugineipes* and *A. insignis* were recorded nesting in every month, and *A. dolichodera* from October to February, seasonal differences either in availability of prey species or in nesting activity are unlikely to be important in explaining differences in prey selection.

Table 7

Seasonal availability of the more abundant actual and potential caterpillar prey species, and nesting periods of three species of *Ammophila* at Hilton.

Wasp and caterpillar species	*Occurrence of caterpillar species or nesting activity in respective month*							
	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Nesting by:								
A. ferrugineipes	+	+	+	+	+	+	+	+
A. insignis	+	+	+	+	+	+	+	+
A. dolichodera	+	+	+	+	+			
Caterpillar species:								
Ligdia pectinicornis	+	+		+			+	+
Lomographa indularia		+		+	+	+		
Omphalucha nr. *ditriba*	+	+	+	+				
Semiothisa/Tephrina	+	+	+	+	+	+	+	+
Syndromodes invenusta	+	+	+	+	+	+		
Xylopteryx arcuata		+		+	+			
X. prasinaria	+	+		+	+	+		
Zamarada spp.	+	+	+	+	+	+		
Geom 6	+	+		+	+	+	+	
Blenina squamifera	+	+	+	+	+	+	+	+
Eutelia adulatrix	+	+		+	+	+	+	
Hypocala rostrata	+	+		+	+	+		
Hypoplexia externa	+	+					+	+
Ulotrichopus catocala		+		+	+		+	
Noct Z				+	+		+	+
Beralade prompta	+	+	+	+	+		+	+
Morasa modesta		+		+	+		+	
Maenas vocula	+	+	+	+			+	+
Orna nebulosa	+	+		+	+	+	+	
Anthene spp.	+			+	+	+		
Arge sp.		+		+		+		

The relative overall abundance of the caterpillar species was determined by combining the results of all samples obtained during beating and comparing them with the frequency with which the species appeared in samples of prey taken by *Ammophila*. The results are shown in Fig. 5 and have a strong positive correlation (r = 0,830). The species of *Ammophila* were therefore preying on the most abundant caterpillars occurring within their respective hunting habitats.

Prey instar

Early instars of several species of caterpillars which grew to a large size, eg. the noctuids *Ulotrichopus catocala*, *Autophlebia bracteata*, *Ophiusa tirhaca* and *Sphingomorpha chlorea*, were never recorded as prey. The majority of caterpillars taken were apparently mature specimens in their final instars. This observation is supported by the data in Figs 3 and 4 which show that maximum sizes attained by prey species seldom exceeded the maximum size taken by *Ammophila*. Some prey caterpillars were in fact almost prepupal, there having been several instances of prey "attempting" to pupate.

Prey specialisation by individuals

Being a mass provisioner, *A. insignis* was the only multiple-prey species for which the entire contents of fully provisioned nests could be identified with certainty. Out of 25 such nests, 48 per cent were provisioned with a single species of prey, 32 per cent with two species and 20 per cent with three. There was also a tendency for successive nests of individual wasps to be provisioned with the same species of prey. This is illustrated by observations of marked females nesting simultaneously at the same site (Table 8). Further, different wasps were taking different species

TABLE 8

Prey usage by individual *Ammophila insignis* at Hilton.

Wasp number	Nest ref.	*Number of respective species of prey in nest*					
		Axiodes bifasciata	*Hypoplexia externa*	*Cucullia consimilis*	Noct Z	*Ulotrichopus primulina*	Noct J
1	379	0	0	0	7	0	0
2	362	4	1	0	0	0	0
	370	1	0	0	1	0	1
	371	4	0	0	0	0	0
4	367	0	1	0	2	0	0
	383	1	0	1	0	1	0
6	369	0	0	4	0	0	0
	375	0	0	0	1	0	1
	381	0	0	5	0	0	0
	385	0	0	2	0	0	0
10	384	0	2	0	0	0	0
11	387	2	0	0	0	0	0

of caterpillars even though they were hunting on the same plant species, as demonstrated by wasps #2 and #6. Thus, although wasps were preying on the more abundant caterpillar species, these were not being taken with the same frequencies by different individuals. The limited nature of the data available makes it impossible to state whether this reflected individual preferences on the part of wasps or was of a more temporary nature, perhaps reflecting localised concentrations of prey to which individuals were repeatedly returning.

DISCUSSION

Prey specificity can often be demonstrated in the field. However, the factors which govern prey selection are not always readily apparent. O'Neill and Evans (1982) could not explain the ultimate cause of prey partitioning between four sympatric species of the sphecid genus *Philanthus*, except for some divergences in prey size due to differences in predator size. However, it often transpires that apparent prey preferences are actually the outcome of prey behaviour, size requirements of the predator, differences in the relative abundance of potential prey and in foraging behaviour, or conditioning of the predator to certain prey or hunting environments due to flexibility in the behaviour of the wasps (Coville, 1976; McQueen, 1979; Laing, 1979; Gwynne, 1981).

The present study has revealed a remarkable lack of overlap in prey species taken by several sympatric species of *Ammophila*. The fact that the size of prey taken, within broad limits, was governed by wasp size and provisioning strategy does not necessarily account for the observed partitioning of prey species. Caterpillars pass through a wide range of sizes during their development and therefore the early instars of large species should theoretically be suitable for the smaller species of *Ammophila* or those employing multiple-prey provisioning. Observations made in the present study suggest that *Ammophila* prey on caterpillars approaching maturity. It is not known whether this is the result of their selection of mature caterpillars or whether such caterpillars are easier to locate or catch. Similarly, Jennings and Houseweart (1984) reported that certain Eumenidae select late instar caterpillars for provisioning their nests but did not offer any explanation.

Nevertheless, the present study shows that the major factor governing this apparent preference for prey species was hunting-habitat selection. Similar findings have been published for species of the sphecid genera *Sceliphron* and *Chalybion* (Muma and Jeffers, 1945), two species of the pompilid genus *Anoplius* (Evans, 1953), and for Pompilidae in general (Evans and Yoshimoto, 1962). Bowden (1964) showed how two sympatric species of the sphecid genus *Dasyproctus* differed by hunting over grass or amongst shrubs respectively. However, the present data indicate only broadly the differences in hunting habitats selected by *Ammophila*. The species of prey taken differ in their location on particular parts of their host plants, suggesting that the wasps themselves are either selecting these microhabitats for hunting or that their prey-size requirements govern whether they must hunt amongst foliage or along stems and branches. Further studies are therefore likely to identify even more discrete interspecific differences in hunting habitats and explain why certain common and apparently suitable prey are not taken.

The discovery of *A. beniniensis* taking prey from below leaf litter at Hilton is of special interest; similar behaviour amongst the Ammophilini is known only from species of *Podalonia*. *A. beniniensis* observed in Natal obtained their caterpillars from trees, never on the ground. Whether or not this is evidence for the existence of two sibling species can only be answered after

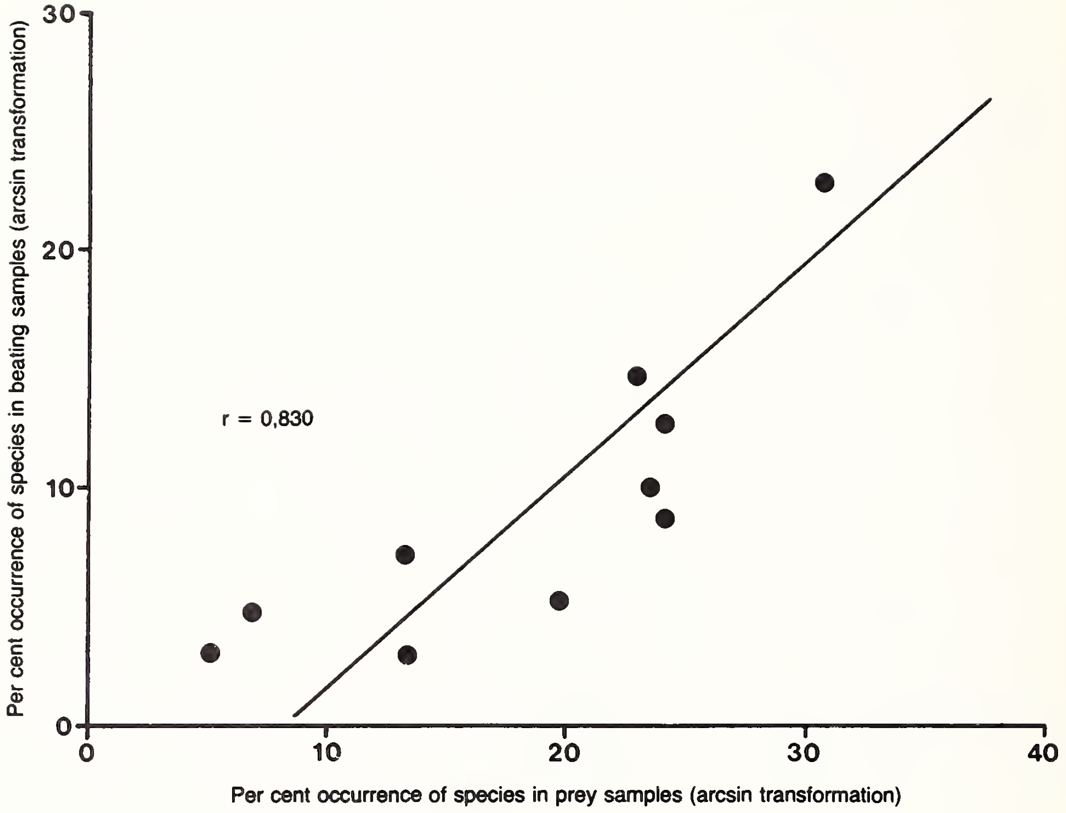


Fig. 5. Correlation between field (beating) and prey samples of ten caterpillar species taken by three species of *Ammophila* at Hilton.

additional studies of their behaviour and taxonomy have been undertaken. Hunting on the ground may have developed in more arid areas, such as in the Eastern Cape, where branch-inhabiting caterpillars may have been forced to spend the day below leaf litter because of increased pressure from predation in the more open vegetation, though this is only speculation. The methods used by *Ammophila* to locate prey are to be discussed in more detail elsewhere, but the fact that wasps initially search on the ground for cues in the form of faecal pellets of caterpillars which indicate the presence of prey in the vegetation overhead (Weaving, 1986) means that such a switch in hunting habitat is perfectly feasible.

The findings for *A. insignis* demonstrate the phenomenon of specialisation on prey species by individual wasps. This has been reported by Tsuneki (1963) for the sphecid genus *Sphex*. Evans (1966) refers to the possibility of conditioning with respect to hunting sites as an explanation. Rather than reflecting individual prey preferences, this is almost certainly the result of locality learning by the wasps, behaviour which would optimise utilisation of spatially heterogeneous prey populations (Rosenheim, in press).

The coexistence of several species of *Ammophila* at Hilton, and at many other sites, inevitably raises the subject of interspecific competition. In spite of differing habitat preferences for nesting (Weaving, 1986), the mobility of the adults would allow the different species to hunt in the same places and therefore compete for prey. However, observations have indicated that it is unlikely that populations of *Ammophila* ever become large enough to cause depletion of their prey resources (unpublished data), though the effects of other caterpillar predators, such as eumenid wasps and birds, and parasitoids would have to be included in any evaluation.

Whether competition could have brought about the observed differences in prey selection cannot be answered here. The data collected in this study provide measures of "actual" niches rather than "virtual" niches as defined by Colwell and Futuyma (1971). These authors stress the importance of obtaining both types of niche measurement before the existence or otherwise of competition can be demonstrated. Overlap of "actual" niches, or lack of it, may be evidence for or against competition (Colwell and Futuyma, 1971; Strong, 1983). The measurement of "virtual" niches requires manipulation of the predator or prey populations; in fact, carefully planned experiments are essential if the existence or otherwise of competition is to be established, and such an investigation was impracticable in the present study. Even so, a clear demonstration of interspecific competition is very difficult to obtain (Connell, 1983). The results have at least shown that any role competition may have played will have been an indirect one through partitioning of the hunting habitat rather than direct partitioning of prey resources. Whether competition or some other factor was responsible for the development of hunting habitat preferences during speciation remains an open question. This topic will be discussed elsewhere with respect to other aspects of nesting behaviour included in a broader study.

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APPENDIX I.

Species of lepidopterous and hymenopterous caterpillars collected from dominant plant species at Hilton.

Family, species, (food plant)	Maximum size prior to pupation mass mg	length mm	Relative abundance	Prey of and per cent
GEOMETRIDAE				
Aphilopota patulata (Mh)	—	28*	16	—
Ascotis selenaria (Ak,Dd,Mh)	734	47	3	—
Axiodes dochmoleuca (Ct)	—	26*	?	Adc 85,7
A. bifasciata (Pi)	208	35	?	Ai 23,2
Comibaena leucospilata (Dd)	—	22*	24	—
Ligdia pectinicornis (Ak)	52	19	10	Af 22,2
Lomographa indularia (Ak)	—	18*	17	Af 0,8
Omphalucha ditriba (Rm)	423	42	19	Ai 0,7
? *Omphalucha* sp. (Rm)	117	26	22	—
Prasinocyma scissaria (Ak)	69	19	21	Af 0,8
Semiothisa/*Tephrina* spp. (Ak)	224	25	2	Af 24,6
Sicyodes spp. (Mh)	145	29	18	—
Syndromodes invenusta (Ak)	34	23	13	Af 11,1
Xylopteryx arcuata (Rm)	120	26	7	—
X. prasinaria (Ml)	226	25	8	—
Zamarada spp. (Ak)	74	19	6	Af 14,3
Geom 6 (Dd)	75	25	1	—
Geom 12 (Lc)	138	31	24	—
Geom 29 (Ml)	279	30	21	—
NOCTUIDAE				
Anua selenaris (Dd)	674	51	24	Ai 0,7
Audea melaleuca (Ak)	832	43	18	Af 1,6 Ai 1,4
Autophlebia bracteata (Dd)	2046	49	19	—
Blenina squamifera (Dd)	237	20	4	Ai 15,2
Craterestra definiens (Pi)	—	—	?	Abr
Cucullia minuta (Ct)	479	34	?	Add 14,7
C. consimilis (Pi)	—	—	?	Ai 17,4
Eutelia adulatrix (Rm)	348	23	15	Ai 6,5
Heliothis armigera (Ct)	—	40*	?	Abr
Hypocala rostrata (Dd)	389	31	17	—
Hypoplexia externa (Lc)	399	28	22	Ai 5,1
Ophiusa tirhaca (Rm)	1573	62	23	—
Sarimarais bicolor (Rm)	580*	38*	24	—
Sphingomorpha chlorea (Ak)	1820	53	21	—
Thria robusta (Ak)	396	30	20	Ab/Pd
Ulotrichopus catocala (Ak)	1161	60	14	—
U. primulina (Ak)	426	42	24	Ai 0,7
LASIOCAMPIDAE				
Beralade prompta (Ak)	609	36	12	Add 47,1

Family, species, (food plant)	Maximum size prior to pupation mass mg	length mm	Relative abundance	Prey of and per cent
Bombycopsis nigrovittata (Ct)	1240	50	?	Add 2,9
Pachypasa truncata (Ak)	—	—	24	—
NOTODONTIDAE				
Morasa modesta (Rm)	581	33	17	—
Porthesia subalba (Ak)	—	17*	18	—
ARCTIIDAE				
Maenas vocula (Ct,Mes)	628	35	?	Add 26,4
LIMACODIDAE				
Coenobasis amoena (Ak)	—	20*	24	—
ZYGAENIDAE				
Orna nebulosa (Mh)	—	12*	5	—
LYCAENIDAE				
Anthene spp.	—	14*	11	Af 15,9
Azanus ubaldus (Ak)	—	12*	24	—
PIERIDAE				
Pieris helice (Ct)	—	—	?	Af 0,8
ARGIDAE (Hymenoptera: Symphyta)				
Arge sp. (Dd)	—	25	9	—

*estimated from photographs.

Abbreviations:—

Plants: Ak — *Acacia karroo; Ct — Chrysocoma tenuifolia; Dd — Diospyros dichrophylla*; Ly — *Lycium campanulatum*; Mes — "mesemb"; Mh — *Maytenus heterophylla*; Ml — *M. linearis*; Pi — *Pentzia incana*; Rm — *Rhus macowanii.*

Wasps: Ab — *Ammophila beniniensis*; Abr — *A. braunsi*; Adc — *A. dolichocephala*; Add — *A. dolichodera*; Af — *A. ferrugineipes*; Ai — *A. insignis*; Pd — *Podalonia canescens.*

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A contribution to the knowledge of the taxonomy and the ethology of the genus *Masarina* Richards (Hymenoptera: Masaridae)

by

F. W. GESS and S. K. GESS

(Albany Museum, Grahamstown)

CONTENTS

ABSTRACT

Descriptions of the female of *Masarina strucki* **sp. nov.**, and the previously undescribed female of *M. hyalinipennis* Richards and male of *M. mixta* Richards are given. A revised key to species is presented. A first account of the nesting of a species of the genus *Masarina* Richards is given. *M. familiaris* Richards nests in vertically presented soil in multicellular nests, attaches the egg to the cell wall and provisions with a wet pollen and nectar mixture. It forages on *Aspalathus* spp. (Leguminosae).

INTRODUCTION

The genus *Masarina* Richards, 1962, endemic to southern Africa, when erected included three species, two of which were known only from one sex. The present taxonomic contribution based on material collected by M. Struck in the Hester Malan Nature Reserve, Springbok and by the Gesses in the Clanwilliam district adds a fourth species, at present known from the female only, and completes the descriptions of the two species previously known from one sex only.

Nothing has hitherto been published regarding the biology of the genus. The data presented are the results of an investigation made during a six day visit to the Clanwilliam district, western Cape Province, South Africa.

TAXONOMIC DESCRIPTIONS (by **F. W. Gess**)

Masarina strucki sp. nov.

FEMALE

Black; a spot at top of tempora behind eyes, a narrow interrupted band along dorsal hind margin of pronotum, a streak on humeral angles, a spot on prepectus, a median spot on posterior half of scutellar disk and a narrow streak along baso-lateral margins of scutellum, transverse posterior bands on tergites 1–5 (somewhat widened medially and at sides), *yellowish-white*. Underside of flagellomeres (especially those composing club), tegulae, distal extremities of femora, entire tibiae and tarsi of all legs, *orange*. Mandibles in part *reddish-brown*.

Length 7,5 mm; length of fore wing 4,9 mm.

Clypeus strongly raised from sides, disk widely and deeply longitudinally depressed, ventral margin trilobed (that is, with a rounded median lobe and on each side a slightly upturned lamellate angular lobe), surface of entire clypeus markedly longitudinally aciculate; frons with its lower third raised laterally and widely depressed medially to match form of clypeus, over most of its area longitudinally aciculate like clypeus. Puncturation of thorax moderate but close, that of abdomen fine but close. Scutellum moderately raised above mesoscutum, falling vertically into a narrow, smooth anterior furrow. Propodeum with obtuse tubercles near top of angles. Tergite 6 transversely impressed distally. Shorter hind tibial spur simple.

MALE unknown.

MATERIAL EXAMINED: [Cape Province:] Namaqualand, [Springbok] 2917 DB, Hester Malan N[ature] R[eserve], 20.viii.1985 (M. Struck) Holotype female.

ETYMOLOGY: The name, in the genitive singular, is formed from the name of the collector of the present specimen, Mr Michael Struck of Hamburg, West Germany, whose help in locating good study areas in the Hester Malan Nature Reserve is hereby gratefully acknowledged.

Masarina hyalinipennis Richards

FEMALE (hitherto undescribed)

Black; small to minute spot on each side of face above ocular sinus, narrow streak at top of tempora behind eyes, tegulae, entire raised disk of scutellum, tergite 1 and 2 (except for anterior declivity of 1, narrow base of 2 and sides of both), a narrow transverse posterior band medially on tergite 3, parts of tibiae of all legs and entire tarsi of fore legs, *various shades of red*.

Length 8,7–9,8 mm (av. of 5: 9,1 mm); length of fore wing 6,8–7,3 mm.

Clypeus moderately raised from sides, disk a little depressed in midline, ventral margin widely and shallowly emarginate with a small, erect, rounded central tooth, lamellate margin wide; surface of clypeus dull, finely aciculate (especially in depression) with moderate punctures becoming closer at sides. Frons similarly finely aciculate (especially medially). Rest of head, thorax and abdomen moderately punctured. Scutellum falling steeply into a wide coarsely crenulate anterior furrow. Propodeal angles weakly developed, almost rounded. Tergite 6 transversely impressed distally. Generally quite similar to the male.

MATERIAL EXAMINED: [Cape Province:] Namaqualand, [Springbok] 2917 DB, Hester Malan N[ature] R[eserve], 20.viii.1985 (M. Struck) 4 females, 28.viii,1985 (M. Struck) 2 males, 25.ix.1986 (M. Struck) 1 female.

***Masarina mixta* Richards**

MALE (hitherto undescribed)

Black; gastral tergites 1–2 *red*, contrasting markedly with rest of tergites. Antennal club beneath, parts of tibiae and tarsi (especially those of fore legs), *orange*. Disk of clypeus, broad supraclypeal marking on face, whole of labrum, proximal half of mandibles, a spot at top of tempora behind eyes, pronotal dorsum medially and humeral angles, *yellowish-white*.

Length 6,5 mm, length of fore wing 4,7 mm.

Like the female characterized by the broad, triangular, black tegulae; other shared characters are the simple shorter hind tibial spur, the scutellum which is anteriorly almost on the same level as the mesoscutum, and the propodeum which has obtuse tubercles near the top of the angles. Tergite 7 only weakly transversely impressed, apically rounded; proximal sternites unmodified. Puncturation similar to that of female.

MATERIAL EXAMINED: Cape Province: Clanwilliam District, Kransvlei (32° 14′ 3″ S, 18° 50′ 49″ E), 7–13.x.1987 (F. W. and S. K. Gess) 1 male; Clanwilliam District, 5 km W of Clanwilliam, road to Graafwater, 12.x.1987 (F. W. and S. K. Gess) 1 female (on flowers of *Aspalathus desertorum* Bol., Leguminosae); Clanwilliam District, Witelskloof (32° 20′ S, 18° 48′ E), 13.x.1987 (F. W. and S.K. Gess) 1 female; Clanwilliam District, Klein Alexandershoek (32° 20′ 20″, 18° 46′ E), 8–13.x.1987 (F. W. and S. K. Gess) 2 females (on ground).

KEY TO THE SPECIES OF *MASARINA* RICHARDS

The present key is based upon that of Richards (1962: 268) but is augmented by the inclusion of the female of *M. strucki* **sp. nov.**, the hitherto unknown male of *M. mixta* Richards and the hitherto unknown female of *M. hyalinipennis* Richards.

1. Tegula black, broad, triangular. Thorax entirely black in female, black except for yellowish-white markings on pronotal dorsum and on humeral angles in male; markings on abdomen reddish, largely confined to tergites 1 and 2 (and in female to parts of corresponding sternites). Shorter hind tibial spur simple. Male with clypeal disk, broad supraclypeal marking on face, whole of labrum and proximal half of mandibles yellowish white; with tergite 2 unmodified and tergite 7 rounded .... *mixta Richards*

— Tegula reddish, long, pyriform. Thorax with at least tip of scutellum reddish or yellow; markings on abdomen reddish, yellow, or both, not confined to first two tergites. Shorter hind tibial spur simple or bifid 2

2. Thorax with yellow markings; abdomen black with narrow yellow posterior bands on tergites 1–5. Shorter hind tibial spur simple. (Male not known.) .... *strucki* **sp. nov.**

— Thorax without yellow markings but with at least tip of scutellum reddish and other markings, if present, of that colour; abdomen with extensive reddish markings and with yellow, if present, confined to lateral or medial spots. Shorter hind tibial spur bifid 3

3. Face on each side above ocular sinus with a large yellow spot; abdomen with yellow markings in addition to reddish ones. Propodeal angles strongly developed, tuberculate.

Scutellum with a narrow smooth anterior furrow. Puncturation of head, thorax and abdomen coarse. Male with clypeal disk and narrow supraclypeal marking on face yellow, labrum black and mandibles largely reddish; with sternite 2 unmodified and with tergite 7 emarginate apically . . . . *familiaris* Richards

— Face on each side above ocular sinus with a small to minute reddish spot (absent in male); abdomen with reddish markings only. Propodeal angles weakly developed, almost rounded. Scutellum with a wide coarsely crenulate anterior furrow. Puncturation of head, thorax and abdomen moderate. Male with clypeal disk and a narrow supraclypeal line on face pure white, labrum and mandibles black; with sternite 2 bearing a bituberculate prominence and with tergite 7 rounded . . . . *hyalinipennis* Richards

SOME ASPECTS OF THE ETHOLOGY OF *MASARINA FAMILIARIS* RICHARDS

Geographic distribution

Masarina familiaris Richards seems to be an essentially south western Cape species with a distribution extending to the fringes of Namaqualand in the north and to Willowmore in the east. Richards (1962) gives collecting records for Camps Bay, Stellenbosch, Ceres, Clanwilliam, Nieuwoudtville, Ladismith and Willowmore.

Additional records (all Albany Museum) are:

Ladismith, 23.ix.1948, 1 female; 24.ix.1948, 1 female; and 26.ix.1948, 1 female (all C.F. Jacot Guillarmod).

Citrusdal, 2.xi.1966 (J. G. Rozen) 1 male.

Clanwilliam District:

Kransvlei (32° 14′ 3″ S, 18° 50′ 49″ E), 7–13.x.1987 (F. W. Gess and S. K. Gess) 9 females, 4 males.

6–9 km N of Paleisheuvel on road to Clanwilliam, 13.x.1987 (F. W. Gess and S. K. Gess) 4 females.

Clanwilliam Dam (32° 11′ 30″ S, 18° 53′ 42″ E), 14.x.1987 (F. W. Gess and S. K. Gess) 10 females, 1 male.

Witelskloof (32° 20′ 35″ S, 18° 48′ E), 13.x.1987 (F. W. Gess and S. K. Gess) 1 male.

Klein Alexandershoek (32° 20′ 20″ S, 18° 46′ E), 28.ix.1985 (F. W. Gess and S. K. Gess) 1 male and 8–13.x.1987 (F. W. Gess and S. K. Gess) 10 females, 5 males.

5 km W of Clanwilliam on road to Graafwater, 12.x.1987 (F. W. Gess and S. K. Gess) 3 females.

Description of the Clanwilliam district

Clanwilliam lies in the Olifants River Valley with to the east the Cederberg Mountains and to the west a hilly area with beyond it the coastal plain. Apart from the sandy coastal plain the whole area is classified geologically as Table Mountain Series. The soils are derived from quartzitic sandstone and shale and are therefore a mixture of sand and clay the proportions of each varying from area to area resulting in their being of variable friability.

The vegetation of the Olifants River Valley to the north of, around and some way to the south of Clanwilliam is described by Acocks (1953) as Veld Type 31, Succulent Karoo, and that further to the south extending almost to Citrusdal as Veld Type 26, Karroid Broken Veld. That of the high lying areas is Veld Type 69, Macchia (Fynbos) and that of the coastal plain is Veld

Type 34, Strandveld. Moll *et al* (1984) re-described the major vegetation categories in and adjacent to the Fynbos Biome. They categorize the area in the immediate vicinity of Clanwilliam a "Mosaic of Dry Mountain Fynbos and Karroid Shrublands" and the high lying areas to the west and east "Mesic Mountain Fynbos", changing to "Dry Mountain Fynbos" further to the west on the fringes of the coastal plain.

The six sites at which *Masarina familiaris* was collected were all characterized by the presence of some Fynbos species and, at the time when the wasps were collected, flowering *Aspalathus* sp./spp. (Leguminosae). Klein Alexandershoek and Witelskloof are situated in Mesic Mountain Fynbos, and the site 6–9 km N of Paleisheuvel and that 5 km W of Clanwilliam on the road to Graafwater are situated in Dry Mountain Fynbos. That at Clanwilliam Dam is a sparsely vegetated slope above the caravan park and that at Kransvlei is a transition area, the vegetation being a mosaic of Succulent Karoo, Karroid Broken Veld and Fynbos.

Plants visited

During the period 7–14.x.1987 a wide range of plants in flower in the Clanwilliam district was sampled for wasp visitors. *Masarina familiaris* was found to be visiting *Aspalathus* spp. (Leguminosae) exclusively. Three species of yellow flowered *Aspalathus*, *Aspalathus desertorum* Bol., *Aspalathus vulnerans* Thunb. and *Aspalathus* sp.(small shrub with ericoid leaves) (Fig. 1) were being visited by both females and males.

Aspalathus desertorum	—Clanwilliam Dam, 10 females, 1 male.
	Klein Alexandershoek, 9 females, 5 males.
	Witelskloof, 1 male.
	6–9 km N of Paleisheuvel, road to Clanwilliam, 3 females.
	5 km W of Clanwilliam on the road to Graafwater, 3 females.
Aspalathus vulnerans	—6–9 km N of Paleisheuvel, road to Clanwilliam, 1 female.
Aspalathus sp.	—Kransvlei, 6 females, 4 males.

Provision

Provision was obtained from nine cells from four nests from two nesting sites. In all instances it was extremely wet and sticky, not forming a distinct "pollen loaf". Pollen in all instances was of one size, 22,5 μ in diameter. When compared with that extracted from flowers of *Aspalathus desertorum* and *Aspalathus* sp. it was found to be identical.

M. familiaris *as a possible pollinator of* Aspalathus desertorum

The flowers of *Aspalathus desertorum* were observed to be visited by the masarid wasps *M. familiaris* and *Ceramius clypeatus* Richards, various bees, beetles and some non-masarid wasps, however, the two masarid wasps seemed to be the only species which penetrated deeply into the flowers and spent any considerable time working in a flower. Whilst gathering pollen but more particularly nectar from these flowers it seems likely that they serve the flowers as pollinators. *M. familiaris* being considerably smaller than *C. clypeatus* is probably the better suited having a better fit to the small flowers.

Description of the nesting sites

Four nesting sites of *Masarina familiaris* were located. Three were at Kransvlei (Figs 1, 2 and 3) and one at Klein Alexandershoek. At all sites nesting was in vertically presented soil, the

Fig. 1. A nesting site of *M. familiaris* Richards, a roadside bank, Kransvlei, 12.x.1987. Positions of nests arrowed. Forage plant, *Aspalathus* sp., in middle distance.

Fig. 2. A nesting site of *M. familiaris* Richards, Kransvlei, 10.x.1987. Two turrets arrowed.

Fig. 3. A nesting site of *M. familiaris* Richards, Kransvlei, 10.x.1987. Two turrets arrowed.

height of the banks varying from 15–100 cm and the nests being excavated at heights of a few centimetres to half a metre. The soil of the nesting sites at Kransvlei is a very hard, non-friable red clay-sand mixture with a relatively high proportion of clay whereas that at Klein Alexandershoek is a relatively friable, sand coloured clay-sand mixture with a relatively low proportion of clay. That at Klein Alexandershoek can, however, with the addition of water be formed into durable "bricks".

The nests occurred singly and also grouped in the vicinity of an old nest suggesting that there is a tendency for newly emerged females to initiate their nests in close proximity to the nest from which they themselves emerged.

Description of the nest

The nest of *M. familiaris* consists of a multicellular burrow with at its entrance a downwardly curved tubular mud turret (Figs 4 and 5). The turret is constructed of mud pellets smoothed on the inside but left rough on the outside. A large number of the interstices are left open so that the turret has a somewhat lacy appearance. The turret and shaft entrance are both of the same diameter. There are one or more sub-horizontal to upwardly or downwardly sloping shafts each ending in a cell (Fig. 5). All those shafts leading to sealed cells are filled with earth (Fig. 5, Nests 3 and 7). A completed nest is finally sealed with a mud-plate at the burrow entrance (Fig. 5, Nest 3). A cell is, over most of its length, of the same diameter as that of the shaft. There is a distinct neck of smaller diameter than that of the cell and shaft. Distally the cell walls slope inwards abruptly to a truncate end wall.

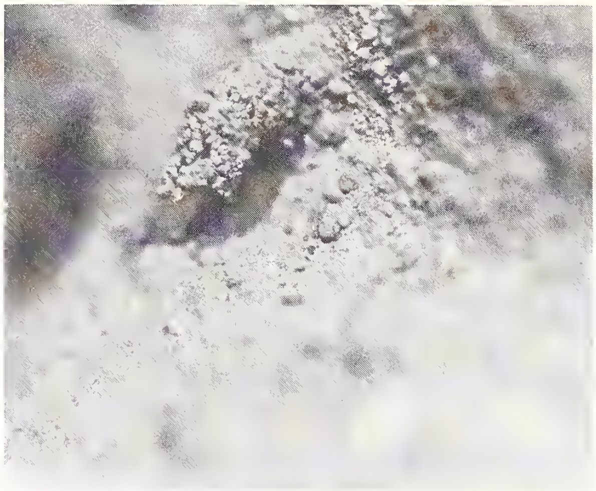

Fig. 4. Turret of *M. familiaris* Richards, the nearer of the two turrets arrowed in Fig. 3. (x 2)

Method of construction of the nest, oviposition and provisioning

Water is required for nest construction. At an early stage in burrow excavation turret construction is initiated using pellets extracted from the excavation. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have the same diameter as that of the shaft, that is 3,5 mm (range 3,5–5 mm, sample of 6). The thickness of the turret wall is 0,5 mm (outer diameter of turret = 4,5 mm, range nil, sample of 5). Almost from the start the additional pellets are added in such a way that the turret curves over and downwards (Fig. 4). After turret construction has been completed further pellets extracted from the excavation are dropped so that they accumulate in a pile at the base of the bank beneath the nest.

The shafts are short and generally slope downwards although they may less commonly slope upwards (in a sample of 15, 13 sloped downwards and 2 upwards). The average angle of slope for the sample was 26°. A shaft is extended without change of angle to end in a cell. Cell excavation is preceded by a reduction of 1 mm in the diameter of the shaft over a short distance to form a neck. After the neck has been created the diameter returns to that of the shaft until the inner end of the cell is approached so that the cell walls are parallel over most of the length of the cell. Shortly before the end of the cell is reached there is a rapid reduction in diameter so that the sides slope inwards to the end of the cell which is truncate, not curved. The average length of the cells of the sample was 11,5 mm.

The excavated cell is very carefully smoothed and shaped so that, although a mud cell is not constructed within it, the walls of the cell are stabilized to such a degree that in nests constructed in relatively friable soil parts at least of the cell walls can be separated from the surrounding soil.

A cell having been constructed an egg is laid at the inner end. The egg is yellow and curved, and is attached by one end to the upper side of the cell so that it lies across the end wall.

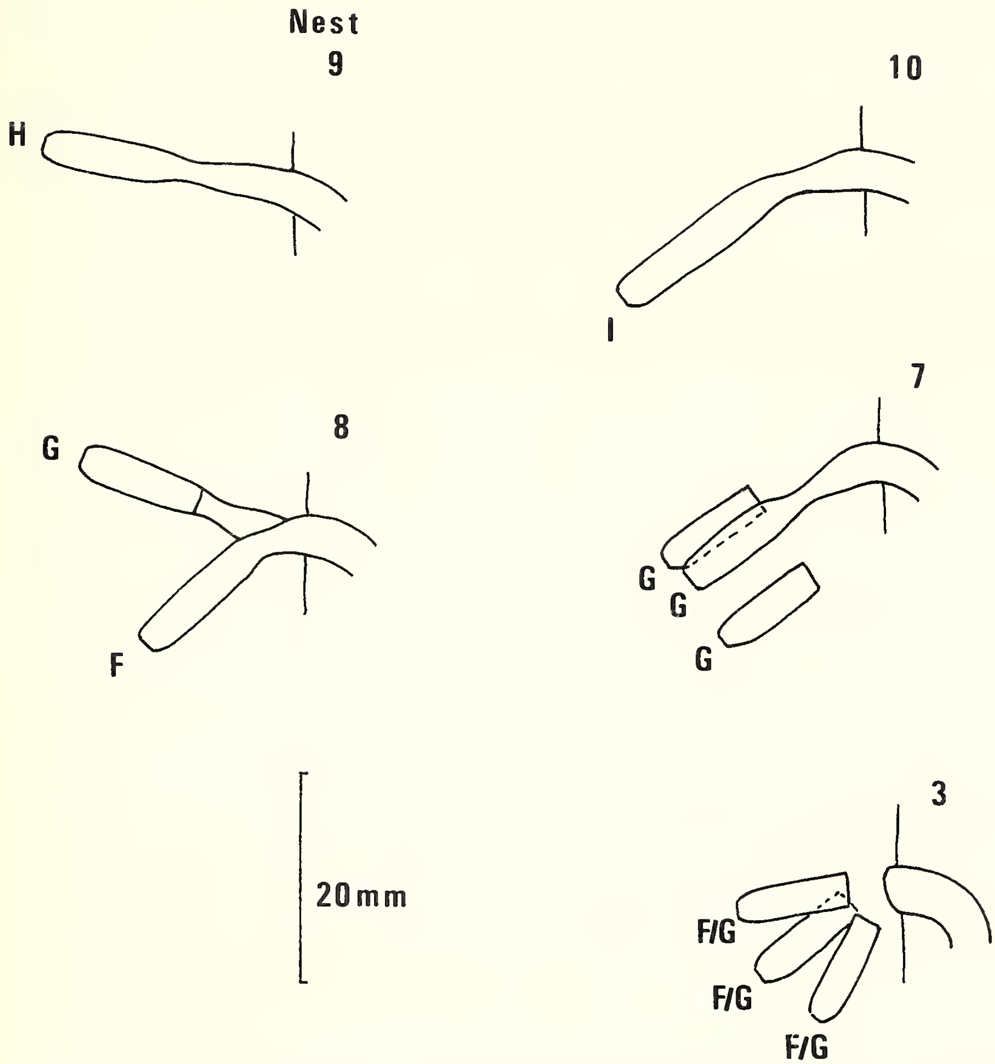

Fig. 5. Vertical plans of the turrets and underground workings of nests of *M. familiaris* Richards. Nests 3, 8, 9 and 10, Kransvlei and Nest 7, Klein Alexandershoek. For key to lettering see Table 1.

After oviposition provisioning takes place. The provision which is a mixture of pollen and nectar is very wet and sticky. Being wet it has no discrete shape of its own. It occupies about two thirds of the cell.

Provisioning having been completed the cell is sealed with a thin mud plate and the shaft is filled with earth. A second shaft is then excavated diverging from the first immediately inside the nest entrance and terminating in a cell which is completed and sealed in the same manner. Several shafts each terminating in a cell may be similarly excavated and completed. When a nest has been completed the burrow entrance is sealed with a mud-plate.

Ten nests were excavated. Of these two were newly initiated nests consisting only of a turret and short shaft, three were single-celled, two two-celled, two three-celled and one four-celled. The nature of the contents of these cells is indicated in Table 1. The cocoon spun by the fully grown larva is firmly attached to the cell walls. There was no indication of nests being used by this wasp for more than one season.

Table 1. Details pertaining to the 10 nests of *Masarina familiaris* excavated in the Clanwilliam district.

Nest No.	Turret	No. of cells	Nature of each cell, cell contents	Remarks
1	Absent	2	A Y	Old nest *Hoplitis* sp. female in nest
2	Present	4	F/G* B/C Z Z	*M.familiaris* female in nest *Hoplitis* sp. in attendance
3	Present	3	F/G*F/G*F/G*	Nest entrance sealed
4	Present	0	—	Newly started nest
5	Present	0	—	Newly started nest
6	Present	1	H	*M.familiaris* female in nest
7	Present	3	G G G	
8	Present	2	G F	
9	Present	1	H	*M.familiaris* female in nest
10	Present	1	I	*M.familiaris* female in nest

Key: * indicates that no egg or larva was found
A. Cell open, containing old cocoon from which adult wasp has emerged.
B. Cell closed, containing pupa in cocoon.
C. Cell closed, containing prepupa in cocoon.
F. Cell either open or closed, containing still feeding immature larva.
G. Cell either open or closed, containing egg with provision.
H. Cell open, containing egg without provision.
I. Cell open, empty.
Y. Old cell containing bee cell.
Z. New cell containing bee cell.

Associated insects

Two of the nests of *M. familiaris* investigated were being attended by a small (6,3 mm long) black bee, *Hoplitis sp.*. One nest (Nest 1) was an old two-celled nest which lacked a turret and the other (Nest 2) was a newly constructed turreted four-celled nest (Table 1). Nest 1 was clearly

an old, disused nest of *M. familiaris* and Nest 2 was a newly constructed nest which was being attended by both the wasp builder and the bee usurper.

The wasp cells utilized by the bee had been widened by the latter prior to the construction of its petal-cells. The petals utilized were those of a purple flowered *Cyanella* sp.(Amaryllidaceae) which was growing in the vicinity. After a petal-cell had been sealed with pieces of petal the excavated cell had been sealed with compacted soil.

Pollen from the provision, a mixture of pollen and nectar, was examined and found to be a mixture derived from three or more plant species. Pollen from *Cyanella* was examined but did not match any of the pollen derived from the bee's cells. Pollen is therefore being collected from different plants from that from which nesting materials are taken.

Male behaviour

Males of *M. familiaris* were observed and collected on flowers of *Aspalathus* spp., however, no interactions between males and females were observed. Males were not seen at nests and as *M. familiaris* has not yet been observed at water it is not known whether the males encounter the females when they are collecting water.

DISCUSSION

As nothing was previously known of the nesting of any member of the genus *Masarina* it seems to be of interest to compare what is now known of the nesting of *M. familiaris* with what is known for other masarids.

The selection of a vertically presented soil surface is behaviourally distinct from the selection of a horizontally presented soil surface (Gess, 1981). The choice by *M. familiaris* of vertical banks for nesting thus distinguishes it behaviourally from the other masarid species known to nest in soil, 15 *Ceramius* spp. (Gess and Gess, 1980, 1986 and 1988), *Jugurtia confusa* Richards (Gess and Gess, 1980), *Quartinioides* sp. (Gess and Gess, 1985 unpublished field notes) and *Paragia tricolor* Smith (Houston, 1984).

The construction of an entrance turret is common to all masarid species recorded nesting in non-friable soil and using water in nest excavation. The only nester in soil not known to construct a turret is *Quartinioides* sp. which nests in friable soil.

The burrow plan of *M. familiaris* is unusual in that access to each cell is from a separate shaft, several shafts each ending in a cell being excavated in turn directly from the nest entrance. The burrow plan of *Ceramius* spp., *Jugurtia confusa* and *Paragia tricolor* is a main shaft with the cells terminating secondary shafts leading from it. Further, the excavated cell of *M. familiaris* differs in shape from those of the other soil nesting species investigated in that the sides are parallel and the diameter is equal to that of the shaft except for a narrow neck and a slight narrowing at the inner end which is truncate. The cell shape of the other species is somewhat ovoid with the diameter over most of the length exceeding that of the shaft and the end wall is rounded.

The egg of all the ground nesting masarids investigated has been recorded as being laid loose in the cell (Gess and Gess, 1980 and 1986, and Houston, 1984) whereas the egg of the aerial nesting *Pseudomasaris edwardsi* (Cresson) (Torchio, 1970) and *Gayella eumenoides* Spin. (Claude-Joseph, 1930 as quoted in Richards, 1962) is attached to the cell wall. It is therefore of interest that the egg of *M. familiaris* nesting in vertical banks, like that of the aerial nesters, is attached to the cell wall.

The provision of *M. familiaris* is very wet and sticky, clearly having a very high nectar content. This seems to be unusual for masarids and, as the cell walls have no obvious waterproofing, surprising. The more usual provision for masarids seems to be a rather dry or tacky loaf with a low nectar content such as has been described for *Ceramius* spp. (Gess and Gess, 1980 and 1986), *Jugurtia confusa* (Gess and Gess, 1980), *Paragia tricolor* (Houston, 1984) and *Pseudomasaris edwardsi* (Torchio, 1970). The only record of another masarid using wet provision seems to be that for *Gayella eumenoides* (Claude-Joseph, 1930 as quoted in Richards, 1962).

Clearly it is premature to draw any conclusions from these comparative comments.

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Historical records of the Wattled Crane *Bugeranus carunculatus* (Gmelin) in the Cape Province and the Orange Free State, South Africa

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CONTENTS

ABSTRACT

Records from the 19th century of the Wattled Crane *Bugeranus carunculatus* (Gmelin) and place names containing the element "kraan" (= crane) in the Cape Province and the Orange Free State, South Africa, are reviewed. Summer breeding is shown to have occurred in the western Cape. Breeding probably occurred in the eastern Cape. There is at least one breeding record from the Transkei. Breeding occurred along the northwestern and northern borders of the Orange Free State and probably more widely before the disturbance caused by the campaigns of Shaka Zulu. The decrease in the southern populations to the point where there is one breeding pair left is attributed to the effects of disturbance by humans and their cattle, starting with the arrival of cattle in the southwestern Cape over 1 800 years ago.

INTRODUCTION AND METHODS

West (1976) and Brooke (1984) pointed out that the Wattled Crane *Bugeranus carunculatus* (Gmelin) was said by early writers to have bred in the western and southern Cape Province, South Africa, but that it no longer did so. There was no attempt to document the former range until the sketch by Vernon and Boshoff (1986 and 1987). This paper attempts to do so in greater

detail by reviewing all pre-20th century records from the Cape Colony and the Orange Free State. In addition, 10 places, the names of which include the element "kraan" (= crane in Afrikaans and Nederlands), have been visited to assess the possibility that they were named after the Wattled Crane (Lelkraanvoël in Afrikaans).

FINDINGS

Western Cape Province

The species was made known to science by Gmelin in 1789, following Latham's work on material from the Cape of Good Hope (Walkinshaw, 1973), but the date of collection and exact provenance of the material is unknown. Thereafter, the first to record the Wattled Crane was Andrew Smith in Roberts (1936) who said "This bird is often seen in marshy ground in different parts of the extensive flats, and appears at a distance to be larger than the *Paradisea* [the Blue Crane *Anthropoides paradiseus* (Lichtenstein)]. It is commonly seen only alone or only with another. . . . Moults during the months of November and December. Lays during the months of November and December, one or two large oval eggs. Builds its nest of grass or reeds in the middle of fleys of water.". Unfortunately, the document is undated so that one cannot be sure what areas (Kirby, 1965) Smith had visited when he wrote. As Roberts (1936) remarked, most of the notes refer to the western Cape at the end of the 1820s but before that Smith had served in the eastern Cape, based in Grahamstown. The authors believe that his remarks apply to both areas and, therefore, these have been quoted under the western Cape which is dealt with first.

Layard (1867: 303), apparently recognizing that this already rare species was threatened by unnecessary approach, was imprecise in his remarks "This great crane is only found in a few favoured localities, scattered over the country. A single pair take up their haunts and maintain it for years, breeding constantly in the same nest, which is repaired as occasion requires. I had the pleasure of watching a pair, through my binoculars, engaged in this proceeding: both birds contributed to the work, stopping now and then to do a little courting, . . . Still 'something came of it,' for my friend Hugo took two glorious eggs out of that selfsame nest, and presented them to me, and they now form part of the treasures of the South African Museum.". It is clear from a study of Layard (1867) that most of his fieldwork took place between Cape Town, Swellendam and Bredasdorp (*cf.* Winterbottom, 1968). Unfortunately, RKB has not found a reference to these eggs in the old egg catalogues of the South African Museum. The authors agree with Dr G. R. McLachlan (pers. comm.), however, that they are probably those of an unlabelled 19th century clutch in the collection. The collection site was probably Soetendalsvlei, south of Bredasdorp, in the midst of the greatest area of marshland in the southwestern Cape. Layard (1867) refers to field work at Soetendalsvlei on pages 35, 67, 311, 342 and 355. The date is given as November 1865 on page 355, indicating that this may have been Layard's only visit. That Hugo was Mr Hugo of Franschhoek, southwestern Cape, and that he also took eggs of the rare Bittern *Botaurus stellaris* at Soetendalsvlei is recorded on page 311.

Sclater (1906) mentions specimens from Caledon and Somerset West (the latter taken in 1857—South African Museum catalogue) and the only record thereafter is of a vagrant seen by R. Hallack on 21 August 1938 at Villiersdorp, Worcester District (Winterbottom, 1979). The authors have been unable to trace the source of the record from Carnarvon mapped in Snow (1978) and have not included it in Fig. 1. It is suggested that it may be a misinterpretation of the Carnarvon Farm, Sterkstroom, record mentioned below.

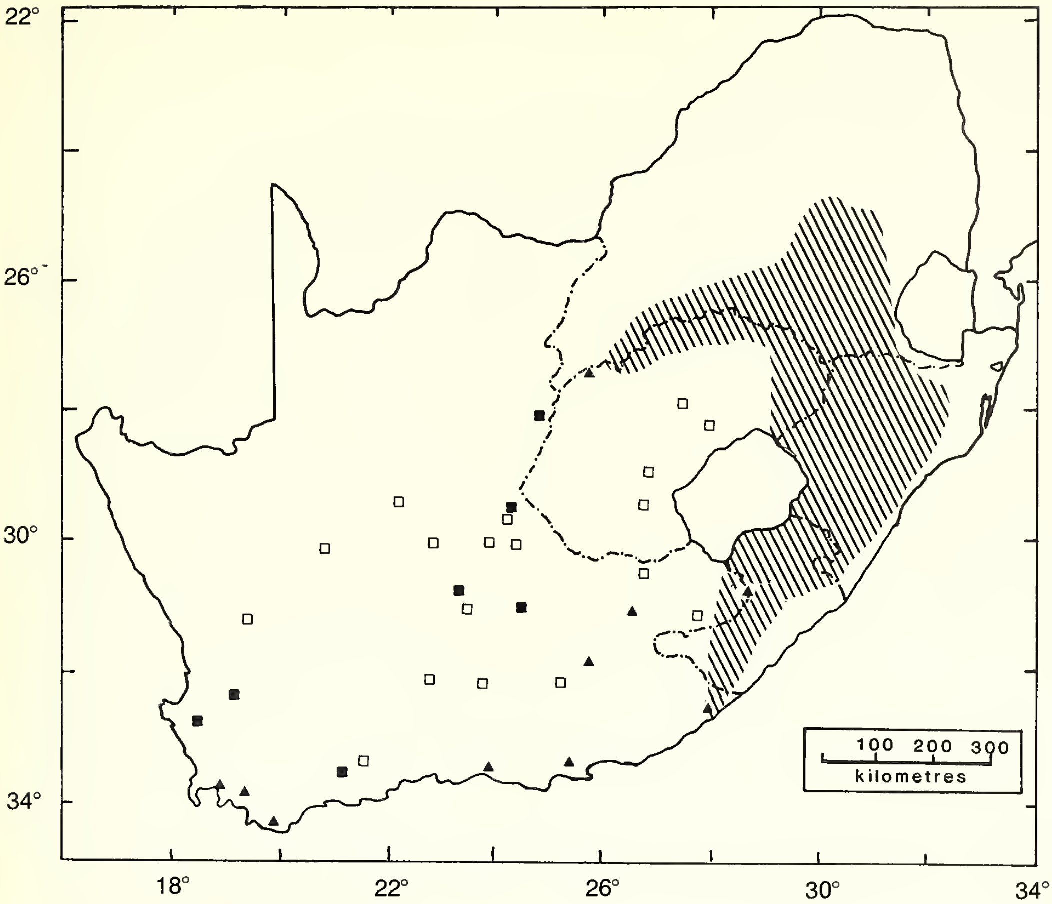

Fig. 1. Map of South Africa showing the approximate location of 19th century Wattled Crane records in the Cape Province, Transkei and Orange Free State (solid triangles) and place names containing the element "kraan" (= crane), solid squares for probable Wattled Crane sites, open squares for probable Blue Crane sites and sites not visited. The shaded area is the post-1970 breeding and nonbreeding range after Brooke (1984).

There are many wetlands in the southwestern Cape apparently suitable for the Wattled Crane and it appears from Layard (1867), supported by Andrew Smith in Roberts (1936), that some of them supported a pair of Wattled Crane. A study of farm and place names sometimes throws light on former distributions (*vide* Skead, 1962; Boshoff and Vernon, 1980). Appendix 1 lists all the place names containing the element "kraan" (= crane in Afrikaans and Nederlands) that the authors have come across in the Cape Province and the Orange Free State: there are none in the Transvaal (P. le S. Milstein pers. comm.). The great majority lie in areas where only the Blue Crane regularly occurs (Fig. 1) and presumably refer to that species.

However, two (Appendix 1) occur in upland valleys in the southwestern Cape which is typical habitat for the Wattled Crane (*vide* Konrad, 1981) but not for the Blue Crane, *viz*. Kraanfontein near the source of the Duiwenhoks River in the Riversdale District and Kraanvoëlfontein by the Leeu River marshes in the Kouebokkeveld of the Ceres District, the visiting of which precipitated this contribution (Brooke, 1987). In addition, there is a possible Wattled Crane site at Kraanvlei in the wheatlands west of Moorreesburg (Appendix 1).

Eastern Cape Province and Transkei

William Burchell seems to have been the first to collect the Wattled Crane in the eastern Cape. Davies and Hull (1983) list two Burchell specimens of this species: Burchell nos B303 and B404; Oxford University Museum nos B/1954 & 5 respectively. Burchell's numbering is sequential or nearly so and B308 was obtained at Graaff-Reinet (Davies and Hull, 1983 as read with McKay, 1943). It is concluded that B303 was obtained somewhere between Middelburg and Graaff-Reinet between 22 March and 12 May 1813 (McKay, 1943). The authors have found no clue to where in the eastern Cape B404 was collected or when but the species with Burchell numbers within five of B404 were taken in an area of vleis, forests and kranses. He spent most time (25 May to 21 June 1813) at Somerset East (McKay, 1943) so the second specimen may have been obtained there. However, there can be no certainty about this as Burchell remained in the eastern Cape until February 1814.

Ludwig Krebs collected two specimens near Uitenhage, probably in 1821 (ffolliott and Liversidge, 1971: 42, 188, 194, 198). ffolliott and Liversidge (1971: 231) record another specimen in Kreb's 12th collection but this is a misinterpretation of Lichtenstein's use of the name *Cracula carunculata* Gmelin which is a junior synonym of *Creatophora cinerea* (Meuschen), the Wattled Starling. However, they interpret Lichtenstein correctly on page 238/9. The two specimens were received in Berlin in 1823 (ffolliott and Liversidge, 1971: 195) and one went to the Naturhistorisches Museum, Vienna, in 1824, being described as from "Caffernland" (H. Schifter *in litt.*, 1987). Krauss (1973) saw Wattled Crane at Cape Tsitsikama in March 1839 and collected a specimen either there or elsewhere (Sharpe, 1894; *cf*. Schüz, 1966). Holub (Holub and von Pelzeln, 1882) saw his first and only Wattled Crane on the Great Fish River north of Cradock, almost certainly in early 1879 when he spent some time in the area during which a drought broke and the river came down in flood (Holub, 1976).

Layard and Sharpe (1884) record that one Wattled Crane was seen by Rickard near East London in about 1880 and they imply that Rickard had seen this species elsewhere in the eastern Cape and the Transkei. Two pairs bred in the years 1885–7 at the source of the Goqwana River (= Gqukunqa River in 3128 BA?) (Godfrey, 1923; Vernon and Boshoff, 1986, 1987), the only certain 19th century record from the Transkei. Another specimen was obtained from Cradock in 1893 according to an old catalogue in the Port Elizabeth Museum. In the 1890s Wood (1896) was told of its presence in the Aliwal North District but did not meet it himself (*cf*. the number of "kraan" names in this district in Appendix 1). It was collected on Carnarvon Farm east of Sterkstroom, in 1899 (Schönland, 1900; Skead, 1967). Unfortunately, this record was erroneously mapped in Brooke (1984) as from Douglas in the northern Cape. It was also collected at East London in 1899 and this specimen is now in the Albany Museum, Grahamstown.

Davies (1907) mentions a young Wattled Crane taken from a nest near Lusikisiki, Transkei, a few years before. While this is not unequivocal evidence for a 19th century breeding site, it is highly suggestive since the Wattled Crane is site tenacious (Tarboton, 1984). It is also possible

that some of the 20th century records listed in Vernon and Boshoff (1986 and 1987) imply 19th century breeding sites but this suggestion is not pursued further in the absence of positive indications. About 1960 W. R. Siegfried (pers. comm.) saw a very large, old nest in a marsh near Swartberg (*cf.* Shephard, 1962), then in the Transkei but now in Natal. The site was probably in use in the 19th century.

A survey of some "kraan" place names in the northeastern Karoo by CJV has revealed (Appendix 1) three places apparently named for the Wattled Crane, viz. Kraanvoëlfontein by Kraankuil Railway Siding, Hopetown District; Kraanvoëlvlei on the Seekoei River, Richmond District; Kraanvoëlvlei at the junction of the Ongers River and the Brak River, Victoria West District. The last is the most westerley suspected Wattled Crane site in the eastern Karoo. The four degree squares 2930/2324 contain many "kraan" place names (Appendix 1) and it has not proved practical to show all of them in Fig. 1.

Northern Cape Province and Orange Free State

A Wattled Crane and two eggs were collected on the Vaal River at Oppermansdrif in the Bloemhof area in the winter of 1838 (Skead and Brandt, 1968; ffolliott and Liversidge, 1971: 123, 248/9, 256). However, the eggs are attributed to *Ardea paradisea* Lichtenstein (= the Blue Crane *Anthropoides paradiseus*—note that *Anthropoides* is masculine contrary to the usage of South African books) by ffolliott and Liversidge (1971: 258) which casts doubt on the identification. Leyland (1972) saw 60–80 Wattled Crane flying by the Vaal River in September 1850, probably between Warrenton and Barkly West. Windsorton lying between these two towns on the Vaal River and Windsorton Road on the main railway line are linked by a farm Kraanvoëlvlei (Appendix 1) which is probably an allusion to the presence of Wattled Crane in the area. G. A. Phillips found a nest with two eggs about to hatch in a very large lagoon near the Vaal River (which side?) (Gurney, 1868). The South African Museum has a specimen from Harrismith taken on 4 November 1917. Snow (1978) mapped a record from west of Mafikeng but the authors have not traced the source of that record and have not mapped it in Fig. 1. Brooke (1984) mapped a record from Douglas but, as noted above, this was in error and the specimen was actually from east of Sterkstroom in the eastern Cape.

DISCUSSION AND CONCLUSIONS

The data presented above show that the Wattled Crane bred in the southwestern Cape, the Transkei and the northwestern Orange Free State in the last century. The eastern Cape records might all be of vagrants but this is taking an extreme position. It is much more likely that it also bred in that area as one pair still does near Ugie (Vernon and Boshoff, 1986 and 1987) and as implied by Andrew Smith in Roberts (1936). Winterbottom's (1968) dictum in his western Cape checklist that it was only a vagrant in the western Cape is not supported. Contrary to the belief of Collar and Stuart (1985) it did occur on the peripheries of the Orange Free State historically and perhaps more widely than is presently known. However, the evidence for historical occurrence in the Orange Free State is found in obscure sources which Collar and Stuart (1985) could easily have overlooked when working on an Afrotropical basis.

The fringe of records in the Vaal valley and in the northeastern Karoo suggests that before 1800 AD the Wattled Crane occurred in suitable habitat throughout the Orange Free State and Lesotho, linking up with the populations occurring around the main Drakensberg massif in the northeastern Cape Province, Transkei, Natal and the eastern Transvaal. There was massive

disturbance of the Orange Free State and Lesotho early in the 19th century arising from the campaigns of Shake Zulu. It seems likely that as a by-product Wattled Crane populations were exterminated or driven away so that virtually none were reported by the earliest naturalists to travel in those areas.

Drainage and human disturbance (Brooke, 1984; Tarboton, 1984; detailed in Vernon and Boshoff, 1986 and 1987) have driven the Wattled Crane from all three areas studied in this paper but earlier European settlement in the western Cape probably ensured that that area was the first to lose its breeding Wattled Crane populations, probably by 1875 or 1880. However, it is possible to look further back into the history of decrease. There are many wetlands in the southwestern Cape which seem suitable habitats for the Wattled Crane. Konrad (1981) showed that its principal foods were rhizomes and bulbs of *Cyperus, Eleocharis* and *Nymphaea*. Southern Cape Province wetlands contain great numbers of *Cyperus* and lesser numbers of other rhizomatous plants including *Eleocharis, Aponogeton* and *Nymphaea* (Bond and Goldblatt, 1984). Thus food was not, apparently, a limiting factor in its historical distribution.

However, the few published references to the Wattled Crane in the early period show that it was then rare, as stated by Latham in Walkinshaw (1973) when first describing the species in English in 1785. In the southwestern Cape the major wetlands are in coastal areas whereas in the mountains the wetlands are smaller, being often large enough for only a single pair each. Wattled Crane usually laid eggs in November and December (Andrew Smith in Roberts, 1936, *cf.* the argument for the Soetendalsvlei breeding site above) at a time when the winter-rain-induced vegetation of the lowlands was drying out. The peak in egg laying between May and August (Maclean, 1985) refers only to the summer rainfall areas where it now lives. Cattle had been owned by the Khoi since *c* 100 AD (Deacon, 1986) and these used to be driven into the marshes in summer to forage. The Khoi also camped by the marshes and foraged freely for tubers etc. in and around them (Schapera, 1930). The resulting disturbance presumably made most coastal wetlands unacceptable to the Wattled Crane (Tarboton, 1984). Thus the decrease in the Cape Province's population of Wattled Crane probably started some 1 800 years ago and the 19th century merely saw the virtual end of a long process of local extinctions induced by sensitivity to disturbance by cattle herders and food gatherers.

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APPENDIX 1

Annotated list of Cape Province and Orange Free State place names containing "Kraan": spelling in the Afrikaans mode.

Place Name	Administrative District	Location
Groot Kraanvoëlkuil	Beaufort West	32° 31′S, 22° 53′E
Klein Kraanvoëlkuil	Beaufort West	32° 27′S, 22° 57′E
Kraanberg	Aliwal North	30° 47′S, 26° 34′E
Now known as Kramberg: there are other Kraanberg in 3026 AD, 3026 DA and 3026 DC, sometimes also called Kramberg.		
Kraanfontein	Riversdale	33° 59′S, 21° 07′E
Many small marshes along the headwaters of the Duiwenhoks River in the southern foothills of the Langeberg. Not Blue Crane habitat but possible for the Wattled Crane.		
Kraanfontein	Ladismith	33° 41′S, 21° 29′E
A hilltop subdivision of Kroonfontein!		
Kraankuil	Calvinia	31° 30′S, 19° 30′E
Now dry open karoo. Not a Wattled Crane site but probably a former Blue Crane site.		
Kraankuil	Calvinia	3020 BD
Kraankuil	Elliot	31° 25′S, 27° 31′E
Kraankuil Siding	Hopetown	29° 53′S, 24° 12′E
Apparently called after the virtually adjacent Kraanvoëlfontein *q.v.*		
Kraankuil	Philipstown	30° 17′S, 24° 13′E
Also known as Kraanvoëlkuil.		
Kraankuilsdam	Hopetown	29° 53′S, 24° 11′E
Kraanvlei	Malmesbury	33° 07′S, 18° 32′E
Now a seasonal marsh after 200 years of wheat cultivation but large enough, when perennial, for the Wattled Crane.		
Kraanvoël Siding	Bloemfontein	29° 13′S, 26° 34′E
Kraanvoëlfontein	Ceres	32° 49′S, 19° 16′E
An upland valley with extensive marshes along the Leeu River and an undoubted Wattled Crane site.		
Kraanvoëlfontein	Hopetown	29° 43′S, 24° 13′E
Now a large vlei with a dam, presumably covering the original kuil (= pool). A probable Wattle Crane site.		
Kraanvoëlfontein	Philipstown	29° 50′S, 24° 20′E
Kraanvoëlkuil	Aberdeen	32° 26′S, 23° 47′E

Place Name	Administrative District	Location
Kraanvoëlkuil road halt	Beaufort West	32° 31′S, 22° 53′E
Kraanvoëlkuil	Britstown	30° 19′S, 23° 50′E
Now heavily eroded but the geomorphology does not suggest a former wetland on the Honderblafspruit able to support the Wattled Crane. A probable former Blue Crane site.		
Kraanvoëlkuil	Pearston	32° 37′S, 25° 04′E
Kraanvoëlkuil	Philipstown	30° 16′S, 23° 49′E
Kraanvoëlkuil	Philipstown	30° 17′S, 24° 13′E
Also known as Kraankuil.		
Kraanvoëlpan	Prieska	29° 43′S, 22° 02′E
A small pan in currently overgrazed veld. A probable former Blue Crane site but not big enough for the Wattled Crane.		
Kraanvoëlsvlakte	Winburg	2827 CA
Kraanvoëlvlei	Dewetsdorp	29° 38′S, 26° 32′E
Kraanvoëlvlei	Ventersberg	28° 04′S, 27° 08′E
Kraanvoëlvlei	Kimberley	28° 21′S, 24° 46′E
Not visited but a probable Wattled Crane site: see text.		
Kraanvoëlvlei	Richmond	31° 23′S, 24° 19′E
A section of the Seekoei River the geomorphology of the valley of which suggests that there used to be vleis along it of a size suitable for the Wattled Crane.		
Kraanvoëlvlei	Victoria West	31° 03′S, 23° 13′E
The junction of the Ongers River and Brak River where the geomorphology suggests the existence of a former wetland large enough to support the Wattled Crane.		
Kraanvoëlvlei	Victoria West	31° 18′S, 23° 27′E
Now flat eroded shale karoo in which the Wattled Crane could never have lived. A probable former Blue Crane site.		

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